COMPARISONS OF SPECIES DIVERSITY, DENSITY AND NICHE USE OF THE TERRESTRIAL AVIFAUNA OF GULL ISLAND AND SOUTH HEAD, WITLESS BAY, NEWFOUNDLAND

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by

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ABSTRACT

Islands usually have lowered species diversity relative to similar areas of mainland. Such changes in species diversity usually lead to changes in bird density and niche use. A study was done on the terrestrial avifauna of Gull Island and the adjacent mainland, South Head, Witless Bay, Newfoundland, to investigate this. It also examined possible specific effects of changes in species diversity on the density and niche use of the island avifauna.

Gull Island had a lower bird diversity than South Head as well as an absence of congeners. Total bird density was also lower on the island. The Northern Waterthrush, Boreal Chickadee and Gray-cheeked Thrush were more abundant on the island, presumably as a response to lowered competition. The Fox Sparrow and Pine Siskin had similar densities at each area. The other species had higher densities on the mainland.

Niche shifts were noted in breeding and foraging habitats of some selected island populations. The Fox Sparrow and Northern Waterthrush shifted their selection of breeding habitat towards the predominant habitat types of Gull Island. The foraging niche of the Boreal Chickadee showed similar flexibility.

The Boreal and Black-capped Chickadees were found in the same foraging habitat on South Head. They coexisted by exploiting different areas of the vegetation. On Gull Island only the Boreal Chickadee was present. It shifted its foraging towards some of the areas exploited by the Black-capped Chickadee on the mainland and broadened its foraging range in other areas. In all three chickadee populations seasonal changes were noted in foraging behavior.

This study supports the hypothesis that species diversity changes on Gull Island led to corresponding changes in density and niche use of all species examined.

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INTRODUCTION

Characteristically islands have impoverished biotas (e.g. Lack and Southern, 1949; Anderson 1960; Preston 1962; Crowell 1963; Grant 1966b; Diamond 1969; Keast 1970; Lack 1966,1969,1976; MacArthur 1971). In some cases ecological types or taxonomic groups common on adjacent mainlands might be missing from an island altogether (Keast 1970). The main purpose of this study was to determine if this was the case for Gull Island and if so how it affected density and niche use of the birds which did occur. The term niche use is used to differentiate the actual foraging behaviors and habitats occupied by the species in this study from the possible wider range of foraging behaviors and habitats each species might occupyunder some other set of conditions.

A number of suggestions have been put forward to explain this insular sparsity of species: degree of isolation, time of isolation and size of island. Traditionally, isolation and time have been used to explain reduced insular faunas. Remoteness from a mainland source may make invasion unlikely or impossible. The number of species on an isolated island should grow with time as the chances of a species reaching such an island increase with time MacArthur and Wilson 1963). Undoubtedly with increased isolation dispersal should gradually decrease (Hamilton and Rubinoff 1963). Anderson (1960) suggests that if an island is colonized by waifs the effect of isolation should be due mostly to the rigid selection involved in the waifing process. MacArthur and Wilson (1963) have made isolation an integral part of their equilibrium model. Other authors have discarded isolation as being of little consequence (Crowell 1963; Lack 1969; Morse 1971,1977) although in the cases they mentioned distances were not extremely great. For example Lack (1969) reports that nine-tenths of the British birds not breeding in Ireland have been observed in Ireland or have occasionally bred there. In this case dispersal does not appear to be a problem. Similarly

Crowell (1962) suggests that many species have not settled in Bermuda although they have been recorded there. Morse (1971) has observed migratory land birds flying across long stretches of open water in the direction of islands in the state of Maine. He further assumes that these small Maine islands (0.2 to 1.5 ha.) may share a common gene pool with the mainland. He bases this assumption on incomplete banding and recording vocalization data and the existence of a floating population on these islands where only one pair of one to three species are found.

The effect of severe climatic conditions is another factor that may contribute to the paucity of insular faunas (Anderson 1960; MacArthur and Wilson 1963). They assume that adverse weather conditions would lead to increased extinction rates. On the other hand Crowell (1962) and Cody (1971) have suggested that insular climates are more predictable and equable, therefore less severe.

An island's size might also contribute to impoverished biotas. Empirically species diversity tends to decrease with reduction in size of islands (Anderson 1960; Crowell 1962, 1963; MacArthur and Wilson 1963; Diamond 1969; Lack 1969; Power 1976). This is also the case for size of forests (Morse 1971). Decrease in diversity of species with decreasing island size could be achieved by a reduction in the diversity of the habitat. Simplification of the island's habitat might be the result of reduced topographical diversity and edaphic conditions (Anderson 1960; MacArthur and Wilson 1967). A limited range of alternative ecological resources due to limited habitat might exclude species that are specialists in favor of generalists (Lack 1966). Diamond (1969) did find a trend towards increased complexity of habitat with increased area of islands in California. Anderson (1960) and Crowell (1963) suggest that some islands may be too small to support self-perpetuating populations of certain species. Morse (1977) observed that some species only occurred on small Maine islands if the forest size equalled or exceeded the size of the species territory on the mainland. Many species could therefore be excluded due to lack or sparcity of proper habitat or by their inability to establish viable populations.

MacArthur, Recher and Cody (1966) have suggested another factor that may lead to lower diversity. They found that birds from the island of Puerto Rico acted as if their habitat was subdivided into coarse layers while birds on the Panama mainland acted as if their habitat was more finely divided. This layering was not an intrinsic part of the forests as both areas had a similar tropical habitat but appeared to be an effect of ecological interactions among the species present. Each layer supported similar numbers of birds on both island and mainland. Terborgh (1967; c.f. MacArthur 1971) found this to be unimportant in the Peruvian avifauna.

Whereas sympatric congeneric species may be common on the mainland, they are frequently uncommon on islands (Grant 1965a, 1966a, 1968). Congeneric species presumably are more similar ecologically than species of different genera (Grant 1968). Competition would thus be greater among congeners than among non-congeners. Even if the resources of an island are sufficient to support two congeneric species it is possible that the reduction of one resource by exogenous means could eliminate a population which would initially be small due to limited area of the island (Grant 1968). The reduced diversity and abundance of island resources would probably also render two species even more similar in realized niche and greatly increase competition.

The factors which determine which species will be present on an island are open to speculation. According to Morse (1971) it is not the result of one species arriving before another. In his work on migratory wood-warblers (Parulidae) in islands off the coast of Maine, Morse found that an order existed in the way species were excluded from island to island but it was independent of the order of arrival of the species.

Island communities often have higher total bird densities than adjacent mainlands of similar habitat (Grant 1965a, 1966c). Densities may be 20 % to 40 % higher on island than mainland localities (Grant 1965a, 1966a; MacArthur, Diamond and Karr 1972; Diamond 1973). This phenomenon is not restricted to birds and has been observed for other vertebrate groups such as salamanders (*Batrachoseps attenuatus, Aneides lugubris*) (Anderson 1960) and lizards (*Ctenosaura pectinata, Cnemidophorus communis*) (Grant 1966b). The presence of equal or higher densities on islands is usually the result of two or more species having far denser populations on the island than on the mainland (Crowell 1961; Grant 1965a, 1966c; Cody 1971; Morse 1977). Grant (1965a, 1966b) found that two species of birds on Marias Magdelena, in Mexico, made up 40% of the total number of birds. Crowell (1961, 1962) observed that 80% of Bermuda birds consisted of only three species. When these abundant species were common to both island and mainland their island densities were higher than on the mainland. However, total island densities do not always exceed mainland populations. They may be lower or equal to them (MacArthur, Diamond and Karr 1972; Diamond 1970b; Yeaton and Cody 1974). Lower island densities are presumably the result of a reduction in the number of species without concomitant increases in the densities of species which are present.

Lower competition due to the absence of many species seems to be the most frequent explanation for both lower and higher island densities. With the elimination of competitors a particular species can broaden its niche by exploiting a greater range of resources. According to Crowell (1961, 1962), Grant (1965a,1966c), Diamond (1973) and MacArthur, Diamond and Karr (1972) such a broadening of the niche leads to an increase in density relative to the mainland. Inger and Greenburg (1966) found that when one of three species of frog (*Rana*) was removed from a stream in Borneo, one of the two remaining species increased in abundance by a factor of 2 to 4 depending on which species had been removed.

Diamond (1970b) has also used the broadening of the niche to explain lower densities. With lowered competition the species is allowed to expand in suboptimal habitat and in these areas does not maintain the higher mainland densities where competition restricts the species to its optimal habitat. The end result may be a net decrease in density. MacArthur, Diamond and Karr (1972) have found that higher island densities occur when many or most mainland species occur together whereas when densities are lower fewer mainland species are found to be present. Crowell (1962) has suggested that a carrying capacity exists for particular habitats as entities themselves and that when the number of species is reduced there may be an increase in the number of individuals per species. This finding implies that interspecific competition is an important factor in determining the organization of island avifaunas.

A number of other explanations have been given for density differences between island and mainland popupations. Krebs, Keller and Tamarin (1969) suggest that an island may not be big enough to allow a population to regulate its numbers by whatever mechanisms are usually employed by a species and therefore higher densities are achieved. Lower predation pressures may also play a role (Anderson 1960; Grant 1966b,c; Diamond 1970b). Lower densities have been attributed to genetic deterioration in isolated populations, caused by small gene pools, reduced intraspecific and interspecific competition and short survival time of populations (Diamond 1970b, 1973).

Several proximate mechanisms may be involved in the increase of an island population. Colonization of a broader range of habitat undoubtedly occurs (Svardson 1949; Hilden 1965). Crowell (1961, 1962) found that an increase in the density of Bermuda birds was accompanied by a closer spacing of territories of Cardinals (*Richmondena cardinalis* Linnaeus), Catbirds (*Dumetella carolinensis* linnaeus) and White-eyed Vireo (*Vireo griseus* (Boddaert)) rather than by a reduction in territory size, whereas Yeaton and Cody (1974) observed a decrease in territory size of Song Sparrow (*Melospiza melodia* (Wilson)) on Santa Cruz. Morse (1977) similarly observed decreases in territory size of some species on small Maine islands. Different feeding grounds (Tompa 1964; c.f. Grant 1965a) and nesting sites (Svardson 1949) have been acquired by some members of populations of *Larus ridibundus* Linnaeus, *Acrocephalus scirpaceus* (Hermann), and *Delichon urbica* Linnaeus.

The effect of high density on the biomass of an island seems to vary. Often large species are underrepresented relative to the mainland but higher densities of smaller individuals on the island result in a comparable biomass (MacArthur, Diamond and Karr 1972). Some islands however have much higher biomass of birds than comparable mainland habitats (Crowell 1962;Grant 1966b; Morse 1977).

As already mentioned above islands tend to be species-poor. The species that are present on the island may continue to exploit the same habitat (MacArthur, Diamond and Karr 1972) or they may undergo a niche shift (Diamond 1970a,b, 1973, 1978; MacArthur, Diamond and Karr 1972). Schoener (1965) refers to such a broadening of one or more parameters due to the absence of competing species, as "ecological release". The change in niche need not be an expansion but may simply be a shift from one area to another or even a contraction (Morse 1971; MacArthur and Wilson 1967).

Niche shift can occur in a number of areas including the exploitation of a greater range of altitude, habitat, vertical foraging positions, foraging behavior and diets, or a combination of these (Diamond 1970a, 1973, 1978; MacArthur, Diamond and Karr 1972). Altitudinal shifts can occur on islands with proper topographical variation.Diamond (1970a) observed such altitudinal expansions on small Southwestern Pacific islands where some species were absent.

Habitat shifts are common and have been observed on a number of islands including Tasmania (Keast 1970), Bermuda (Crowell 1961, 1962), Puercos (MacArthur, Diamond and Karr 1972), the Canary Islands (Lack and Southern 1949), Madeira (Buxton 1960), the Azores (Marler and Boalman 1951) and Southwest Pacific Islands (Diamond 1970a,b).Crowell 1961 1962) observed increases in habitat exploited on Bermuda even though the forest height of the island was lower than on the mainland.

Vertical shifts occur when a species forages in different vertical strata. Such expansions have been observed by some authors (Diamond 1970a; MacArthur, Diamond and Karr 1972; Cody 1974). Crowell (1962) observed no such increase in the range of foraging heights in birds in Bermuda.

Changes in feeding methods and diets may be the result of reduced competition. Such changes are not as common (Diamond 1970a,b,1973) and were not observed by Crowell (1962) in Bermuda. Sheppard, Klopfer and Oelke (1968) did observe that the feeding behavior of the Bermuda Catbirds and Cardinals were slightly less stereotyped than on the mainland.

Often when a species is on a species-poor island, expansion of the niche other than in diet and foraging behaviors appears to be prompt and does not require morphological change (Diamond 1970b; Cody 1974). Longer isolation may result in genetic changes which could lead to changes in diet, foraging tactics and possibly morphological changes in bill and feet (Crowell 1962; Diamond 1970b; Keast 1970; Cody 1974).

Diamond (1970b) found that half the birds of the island of Katar underwent no shift in niche. In the remaining species expansion of diet and foraging behaviors was the least frequently observed ecological change. Changes in habitat, altitude and vertical foraging positions were much more common.

In the section dealing with niche shift, in this study, emphasis was placed on habitat and foraging area utilized. Altitudinal shifts were not investigated as the topography of the mainland and island did not lend itself to such a study. Changes in diet and foraging behaviors were also ruled out since changes in diet are very likely to be reflected in foraging locality and activity (Hespenheide 1975). Because of the taxonomic diversity in species considered in this study, the emphasis was placed on foraging and nesting sites rather than on foraging behavior.

Gull Island is an offshore island off the island of Newfoundland. It lies close to shore and is small although large enough to support populations of most passerine species on the adjacent mainland.

Most of the research done on the ecology of islands has been restricted to more climatically moderate areas than Newfoundland; e.g. the Western coast of the United States (Anderson 1960; Diamond 1969), the Pacific coast of Mexico and the Gulf of Panama (Grant 1965a,b,1966b,c; MacArthur *et al.* 1973), the Caribbean (MacArthur, Recher and Cody 1966), Bermuda (Crowell 1962, 1963; Sheppard, Klopfer and Oelke 1968) and the Southwest Pacific (Hamilton and Armstrong 1965; Diamond 1970a,b, 1973; Terborgh and Diamond 1970). Although Morse (1977) compared the avifauna of small Maine islands to adjacent mainland, much of the research in northern latitudes has been restricted to the study of single taxa. Morse (1971) studied wood-warblers (Parulidae) on spruce covered islands in Muscongus Bay, Maine. Cody and Cody (1972), working farther north on the Lewis and Shetland Islands, studied territory size, clutch size and food in populations of wrens (*Troglodytes troglodytes* Linnaeus).

Although much work has been done on island ecology this study is different from most in two major ways. First, Gull Island is being compared to another much larger island, Newfoundland. Secondly the study was conducted at a locality further north, in a more severe climate than most other studies of island biogeography, and species diversity tends to decrease from low to high latitudes (Klopfer and MacArthur 1960, 1961; MacArthur and MacArthur 1961; Connell and Orias 1964; MacArthur 1965; Ricklefs 1966; Recher 1969; Emlen 1973). Another difference encountered from temperate to tropical regions is the increase in the proportion of non-passerine birds in the avifauna (Klopfer and MacArthur 1960). It is of interest to see if either or both of these factors lead to smaller ecological differences between the avifauna of shore and island localities than were encountered in other studies.

MATERIALS AND METHODS

Research was conducted on the western half of Gull Island (Witless Bay Sea Bird Sanctuary) (47° 15'N, 52° 46'W) and the adjacent mainland, South Head, Witless Bay, Avalon Peninsula, Newfoundland (47° 17'N, 52° 47'W) (Figure 1). This area lies within the Avalon, Boreal forest region (Rowe 1972).

Gull Island is located 1.6 km from the nearest point of land. It covers an area of 0.95 km^2 and consists of open, grassy areas along the coast ("Puffin slopes", Maunder and Threlfall 1972; and meadows, Haycock 1973) and within the interior, mostly old growth forest. Haycock (1973) also mentions the presence of bogs. Balsam Fir (*Abies balsamea* (L.)Mill.) is the dominant tree species. Dead trees are quite common.

South Head, Witless Bay, comprises open areas (farmer's field, bogs and heaths), especially along the coast, and second growth forest. Balsam Fir is the dominant tree species.

Authorities for scientific names were taken from Fernald (1950) for plant species and from the A.O.U. checklist (1957) for bird species.

I. Bird census

a) Method

Line transects were established at both localities, along preexisting paths (Figures 2 and 3). Markers, made from red yarn, were placed every 15 meters, on trees within the forest and on small shrubs and stakes elsewhere. The transects on the island and mainland measured 1.44 km and 1.62 km respectively. Both open and forested areas were included within the transects. Less than 10% was open on the island whereas

Figure 1. Map of Newfoundland showing location of study area. The inset shows Gull Island and South Head, Witless Bay.

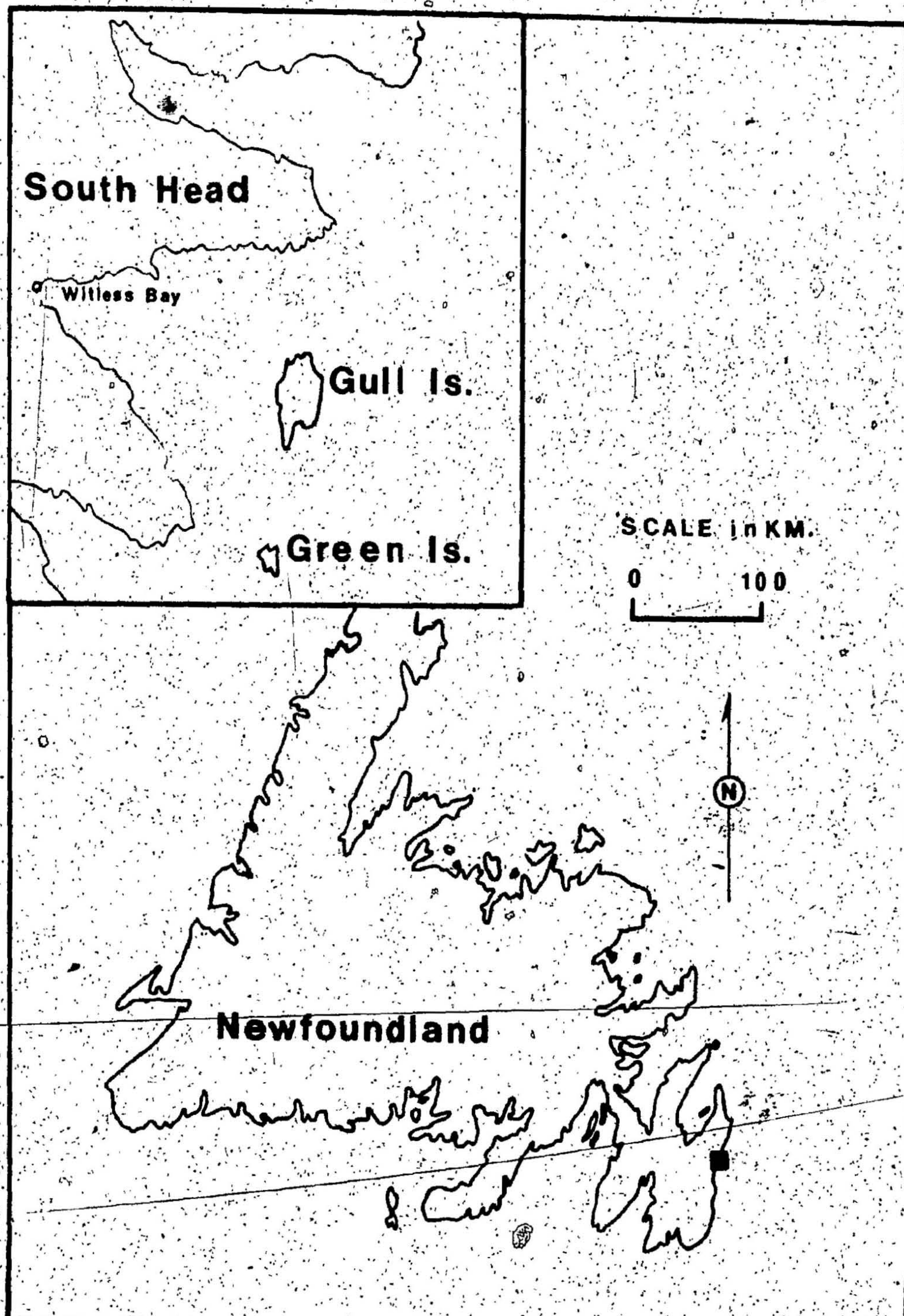

South Head
Witless Bay
Gull Is.
Green Is.
SCALE in KM.
0
100
N
Newfoundland

Figure 2. Map of Gull Island. Dotted line indicates transect area.

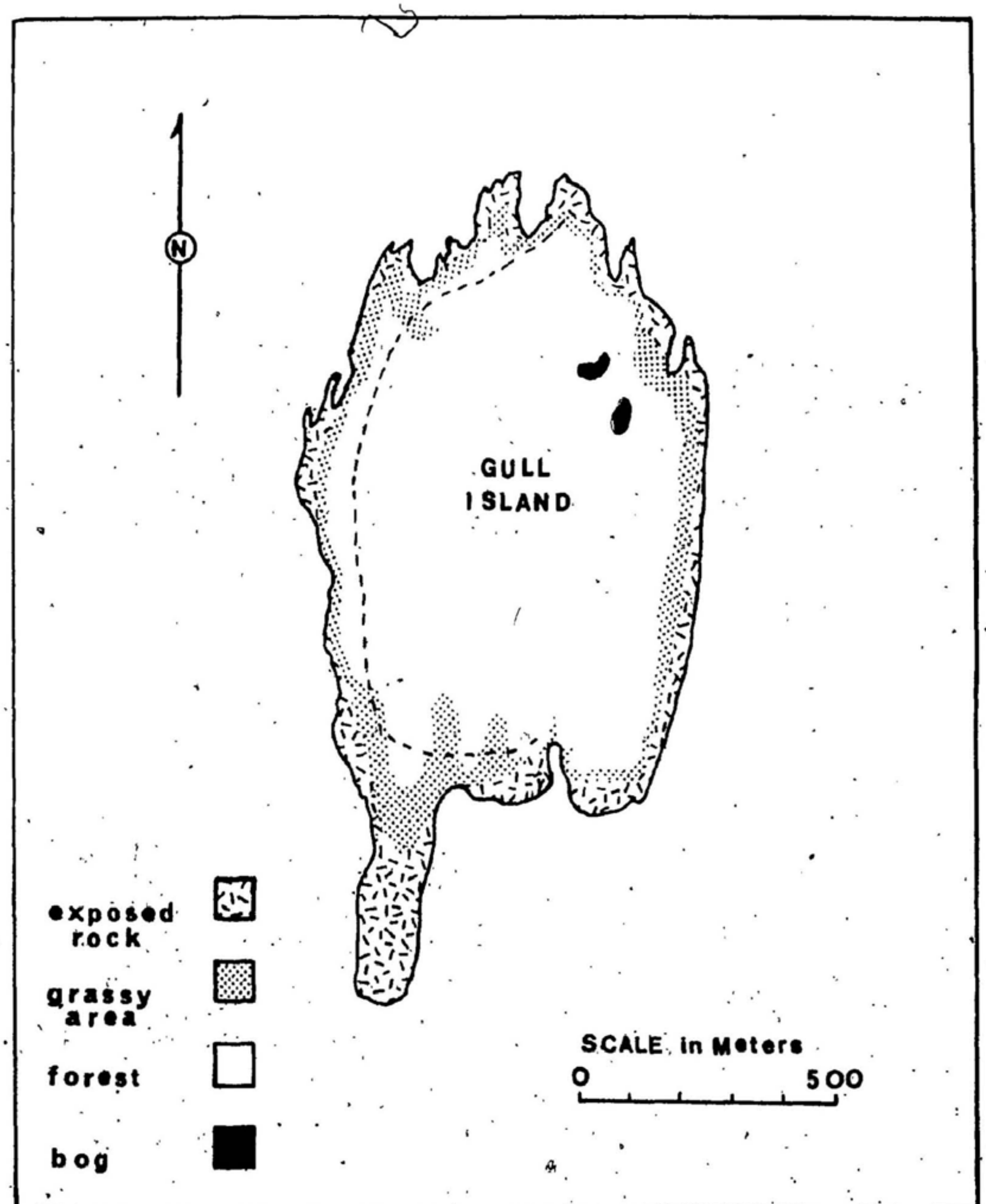
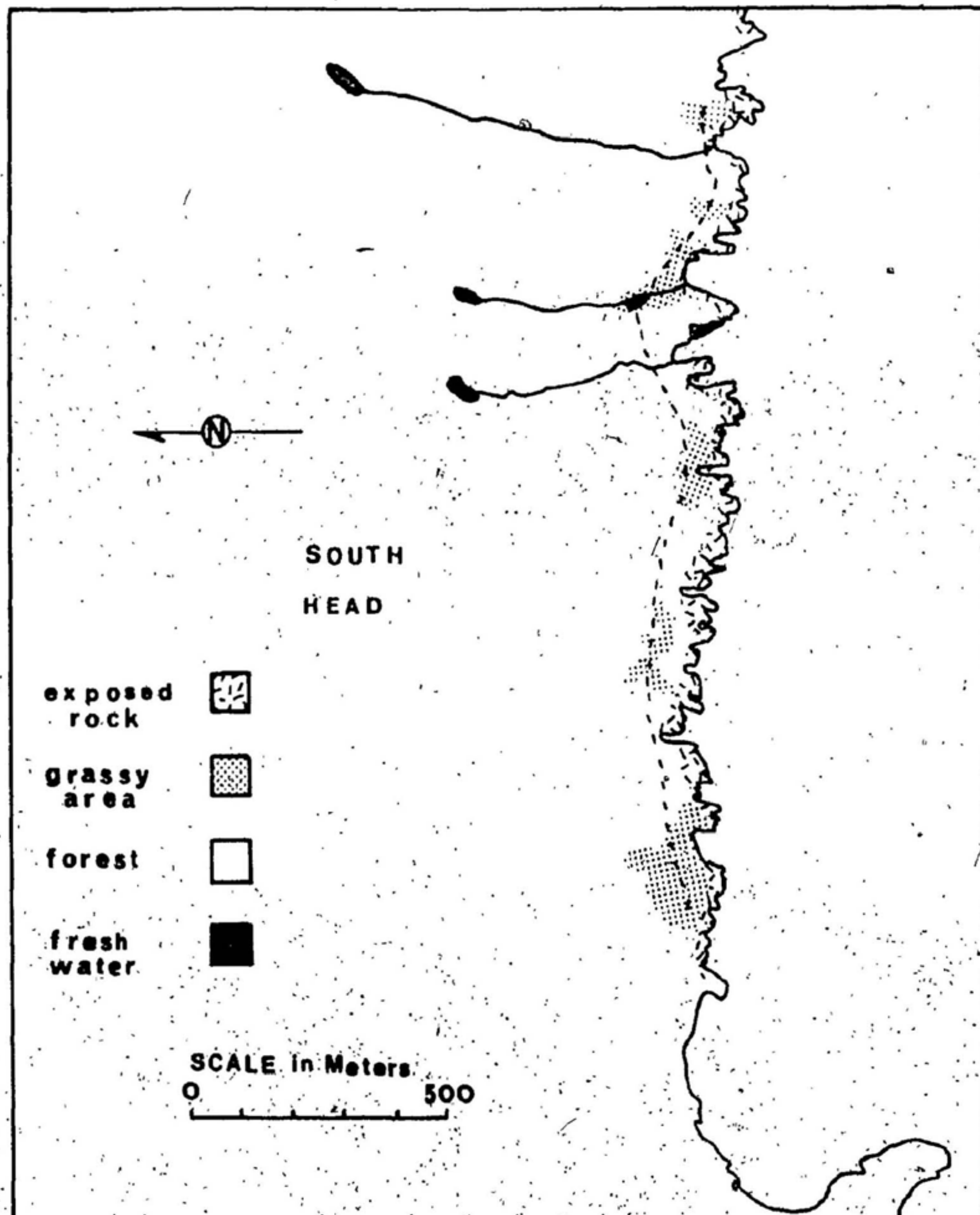

N
GULL
ISLAND
exposed rock
grassy area
forest
bog
SCALE in Meters
0
500

Figure 3. Map of South Head, Witless Bay. Dotted line indicates transect area.


N
SOUTH
HEAD
exposed
rock
grassy
area
forest
fresh
water
SCALE in Meters
0
500

approximately 40% was open on the mainland.

Censuses of passerines were conducted in the morning, beginning within one hour of sunrise. Birds were located either by sight, using 7X50 binoculars, or by sound. Each sighting was recorded on data sheets. Censuses interrupted by adverse weather conditions (e.g. rain, heavy fog) were discarded. A total of 30 censuses were carried out on South Head, Witless Bay, between May 18 and July 19, 1977; 11 were carried out on Gull Island, between June 16 and July 26, 1977.

b) Analysis

Diversity indices were calculated for all census days, for both South Head and Gull Island, using Shannon's Index (Pielou 1966b). This index is a function of the populations of the several species present. It takes into account both number of species and number of individuals per species. Because the underlying distribution of these indices is unknown (Pielou 1966a) a Kruskal-Wallis test (Sokal and Rohlf 1969) was utilized to compare the diversity indices of each locality.

Bird densities were calculated for each census day and each site. They were expressed as birds/km of line transect. It was assumed that the detectibility of the birds on either side of the transect paths was the same within species for each area. These bird density values were then converted to common logarithms. Such a transformation renders the variance of a sample independent of its mean and reduces the weight of the variance where values tend to be very small or large (Sokal and Rohlf 1969). To compare mean monthly densities, for June and July, within each locality, a t-test on the difference between two means (Sokal and Rohlf 1969) was employed to compare the converted log data. A similar test was used to compare total summer densities of the areas.

Densities were also calculated for individual species which were common to both localities and present in sufficient numbers for comparison between localifies. A t-test was used to compare densities within each site (June vs. July) and between sites. When species showed no monthly differences for both sites, total June plus July data were used for comparison. When one or both localities showed monthly variations in a species' density, two comparisons were made, one for each month. Censuses taken during May on South Head were not used because no corresponding counts were carried out on Gull Island.

II. Stucture of the vegetation

a) Method

To establish habitat preference of some bird species, plots were sampled using the method described by James (1971) and James and Shugart (1970). A Biltmore stick was held vertically at arm's length, 11.28 meters from a suspended, brightly colored stick. This colored stick was sighted and the appropriate "length" permanently marked on the Biltmore stick. By suspending the colored stick in a desired area, a circular plot of 0.04 hectares (diameter of 11.28m (37 feet)) was established. The Biltmore Stick, calibrated using the above method, was used to determine whether the observer was within the sampling area.

Tree species and diameter at breast height (established using a Biltmore stick) were determined for all trees within the plots and recorded on data sheets similar to those used by James and Shugart (1970). Trees were classified according to their diameter into the following categories: A (2.54 cm -7.62 cm), B (7.62 cm - 12.70 cm), C (12.70 cm - 17.78 cm), D (17.78 cm -25.40 cm), E (25.40 cm - 30.48 cm), F (30.48 cm - 35.56 cm), G(35.56 cm - 39.64 cm) and H (39.64 cm +).

Shrub density was determined by counting the number of shrubs found in an area the width of outstretched arms on two transects at right angles to each other and passing through the center of the sampling plot (area of 33.5 m^2). Shrubs were defined as trees with a diameter of less than 2.54 cm. They were identified to species.

An ocular tube (made from an empty roll of bathroom tissue with two strings at one end, at right angles to each other, to act as sights) was held directly overhead to determine the presence or absence of canopy. Similarly, readings were taken for ground cover by extending the tube at arm's length and directing it downwards approximately 1.5 meters in front of the observer. Approximately 20 plus or minus readings were taken alternately for canopy and ground cover along two transects, at right angles to each other and passing through the center of the plot. The dominant ground cover plants were also noted.

Maximum canopy height was established using a mirror to which a small level had been attached. The mirror was held at arm's length, 0.91 meter from the ground. The observer walked towards the tallest tree in the plot until the crown appeared in the mirror. The distance from the observer to the tree plus 0.91 meter was approximately equal to the height of the tree (James and Shugart 1970).

Plant censuses, taken along the established line transects, were used to determine the breeding habitats of two of the commonest bird species on both the island and mainland, the Fox Sparrow (*Passerella iliaca* (Merrem)) and Northern Waterthrush (*Seiurus noveboracensis* (Gmelin)). For these two species, the perch of singing males constituted the center of the plot (James 1971). In Northern Waterthrush habitat the presence or absence of water was also noted. For this study breeding habitat therefore constituted a circular plot of 0.04 hectares around the perch of a singing male.

To investigate foraging habitats of the Boreal Chickadee (*Parus hudsonicus* Forster) and Black-capped Chickadee (*P. atricapillus* Linnaeus) on the mainland, and Boreal Chickadee on the island, circular plots were chosen along the line transects, to correspond to the approximate centers of foraging flocks. Census records were used to determine these centers.

The number of samples taken for each species depended on the variability of the habitat. This was determined by sampling until the last two estimates of tree density per .04 ha did not differ by more than 25 trees (James and Shugart 1970).

Seven plots were sampled for the breeding habitat of the Northern Waterthrush at both localities. Six and seven were taken on the island and mainland respectively for the Fox Sparrow. The number of plots sampled for the foraging habitats of chickadees was as follows: eight for the island Boreal Chickadee, seven for the mainland counterpart and nine for the Black-capped Chickadee.

b) Analysis

All data collected on the vegetation structure were compared in the following way. The Waterthrush, Fox Sparrow and Boreal Chickadee were compared to conspecifics between localities. The Black-capped Chickadee, which was not present on Gull Island was compared to the mainland Boreal Chickadee.

Total tree and shrub densities were calculated for all samples and converted to common logarithms. A t-test of the difference between two means was used to detect differences between localities. Where variance appeared different, an equality of variance test (Sokal and Rohlf 1969) was used to see if the localities differed significantly in variance.

To compare tree and shrub composition and structure of different habitats, principal component analysis was used. The program employed was SPSS, Factor Analysis PA1 with Varimax Rotation (Nie *et al.* 1975). This method takes a given set of variables, usually intercorrelated to some extent, and transforms them into a new set of orthogonal axes (components or factors) unrelated to each other (Huntingford 1976; Nie *et al.* 1975). The first factor selected accounts for the most variance possible from the total variance; the second accounts for the greatest possible remaining amount; and so on. All such isolated factors are uncorrelated with each other.

The analysis was not carried out on raw data but on percent occurrence within each sample. The variables for tree composition were species and diameter as mentioned above, and for shrub analysis shrub species. Tree species were the following: Balsam Fir, White Spruce (*Picea glauca* (Moench)Voss), Black Spruce (*P. mariana* (Miller) BSP.), Mountain Alder (*Alnus crispa* (Aiton) Pursh), American White Birch (*Betula papyrifera* Marshall), American Mountain Ash (*Sorbus americana* Marshall), Bartram's Chuckley Pear (*Amelanchier bartramiana* (Taush) Roemer), as well as dead trees. Shrub species consisted of Balsam Fir, White Spruce, Black Spruce, Mountain Maple (*Acer spicatum* Lamarck), Bartram's Chuckley Pear, Northern Wild Raisin (*Viburnum cassinoides* Linnaeus), Pin Cherry (*Prunus* *pensylvanica* Linné), Mountain Holly (*Nemopanthus mucronata* (linnaeus)), as well as one unidentified deciduous species and dead shrubs.

The tree and shrub composition of the habitat of each bird species were compared between localities as mentioned previously to see if differences were present. The Factor Analysis scores were compared, factor by factor, for each bird species or pair of species using a t-test.

To determine if tree and shrub compositions were similar on South Head and Gull Island factor scores were compared, factor by factor, to see if they were distributed similarly at both areas. A mean was taken for each factor on the island and mainland and a t-test utilized to compare them. In cases where the vegetation was not distributed similarly for a particular factor, and this factor was selected differently at each area by a bird species, a further test was done to see if the bird species distributed itself more non-randomly around the average available vegetation at one location than another. The scores of the bird species for that particular factor were compared to the mean score of all samples for the area. The deviations from the mean became the new scores. A t-test was then done to see if differences existed between localities.

Canopy and ground cover were analyzed using the following method. A Kruskal-Wallis test (Sokal and Rohlf 1969) was used to compare each group of birds as mentioned previously. When the total number of positive (+) and negative (-) readings per sample did not equal 20 these (+) and (-) values were converted so that their total would equal 20.

Means and confidence limits (Sokal and Rohlf 1969) were calculated for maximum tree height. The confidence limits were then plotted and examined for overlap. When limits varied greatly in size an equality of variance test (Sokal and Rohlf 1969) was used to check for differences in variance.

III. Foraging behavior

a) Method

The foraging behavior of the Boreal Chickadee and Black-capped Chickadee was investigated. Birds were followed with binoculars from the time first sighted until they flew out of visual range or until the observer terminated observations. The time spent in each foraging category was measured using a stop watch and recorded on a cassette tape recorder (Cody 1974). Three aspects of foraging behavior were investigated: height of foraging, vegetation type and part of the tree used.

1) Height of foraging

Six classes of foraging height were established. All seconds of foraging bouts were roughly classified into these categories: 1) ground (bare ground or low surface vegetation); 2) ground to 0.3 meters (often consisting of low shrubs or dead branches lying on the ground); 3) 0.3 meters < 1.5 meters; 4) 1.5 meters < 3.05 meters; 5) 3.05 meters < 6.1 meters; 6) > 6.1 meters.

2) Vegetation type

Vegetation was divided into three classes:

1) Deciduous vegetation consisted of all live deciduous trees or shrubs. 2) Live evergreen vegetation consisted of all parts of evergreen trees or shrubs, within a few centimeters of green needles. 3) Non-green vegetation included all dead trees or shrubs, deciduous or evergreen,

and trunks, bare branches or limbs of evergreen trees.

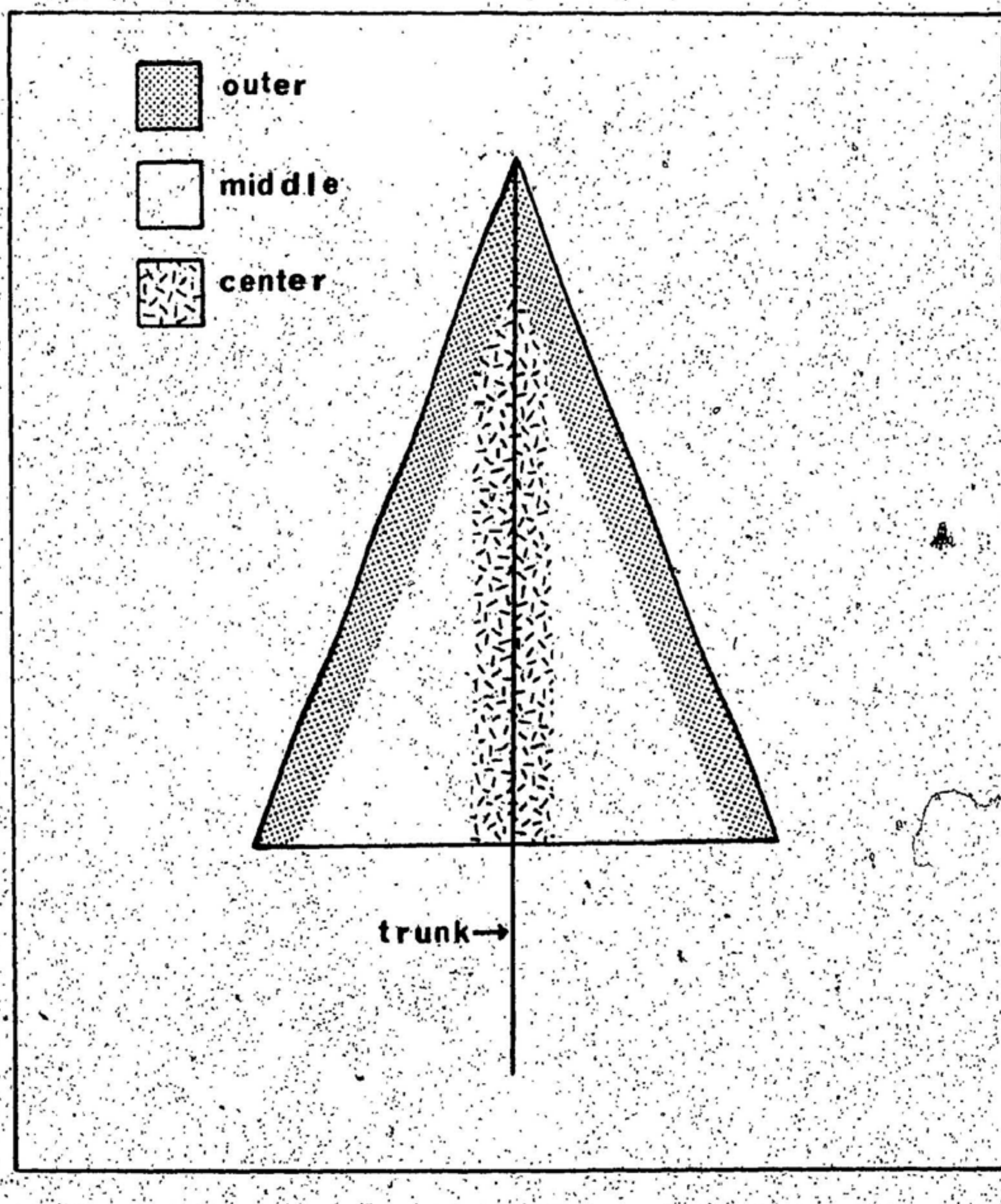
3) Part of tree used

Evergreen trees were divided into 4 regions following MacArthur (1958) (Figure 4): 1) trunk; 2) center (the area close to the trunk, usually devoid of needles); 3) middle (the middle part of limbs where they begin to branch out and which may or may not have green needles); and 4) outer (the peripheral areas of the tree, including the crown, which usually consists mostly of green vegetation).

b) Analysis

Three different types of comparisons were made for each of the three foraging behaviors investigated. The first was made within each population and was seasonal. The summer was divided into two periods, the first from June 9 to June 20, and the second from June 21 to July 20. The second comparison was between the island and mainland Boreal Chickadee and between the Black-capped Chickadee and its mainland congener. Each pair of chickadees was compared for the periods of June 9 to June 20 and June 21 to July 20. Finally the groups were compared using total summer results, by the same comparisons used in the second case. In all the above the method of analysis was the G-test (Sokal and Rohlf 1969), a test for independence of occurrence of discrete events.

Figure 4. Designated areas of evergreen trees used in this study.


outer
middle
center
trunk→

RESULTS

I. Bird census

Islands are usually typified by an impoverished fauna. It was therefore of interest to see if Gull Island followed this same trend. This generality did hold true. Thirteen species of passerines were observed on Gull Island whereas twenty-five species were seen on South Head, Witless Bay, the adjacent mainland (Table 1). These totals were obtained by combining all species seen during morning censuses with observations made at other times of the day, while collecting data on foraging behavior or vegetation structure or while simply walking through the study area. Morning census observations accounted for 22 of the 25 species. The other three species were the Common Raven (*Corvus corax* Linnaeus), Northern Parula (*Parula americana* Linnaeus), and the Rusty Blackbird (*Euphagus carolinus* (Müller)).

The abundance of the species varied. A few were not seen more than twice during the entire summer. This included the three species that were not seen during morning censuses, as well as the following: Eastern Kingbird (*Tyrannus tyrannus* Linnaeus), Red-breasted Nuthatch (*Sitta canadensis* Linnaeus), Golden-crowned Kinglet (*Regulus satrapa* Lichtenstein) and Starling (*Sturnus vulgaris* Linnaeus). From this group of "scarce" species only the Common Raven was observed at both South Head and Gull Island.

Of the 13 observed species on Gull Island, only one, the White-winged Crossbill (*Loxia leucoptera* Gmelin), was not seen during morning censuses. One flock, did however, contain roughly 25 individuals.

Table 1. Passerine birds observed on South Head, Witless Bay and Gull Island, between May 18 and July 26, 1977. (+ observed more than twice; * not observed during morning censuses; t not observed more than twice).

Species	South Head	Gull Island
Eastern Kingbird	t	
Yellow-bellied Flycatcher	+	+
Common Crow	+	
Common Raven	t*	+
Black -capped Chickadee	+	
Boreal Chickadee	+	+
Red-breasted Nuthatch	t	
Brown Creeper		t
Winter Wren		+
Robin	+	+
Gray-cheeked Thrush	+	+
Golden-crowned Kinglet	t	
Starling	t	
Northern Parula	t*	
Blackpoll Warbler	+	+
Northern Waterthrush	+	+
Wilson's Warbler	+	
Rusty Blackbird	t*	
Pine Grosbeak	+	+
Pine Siskin	+	+
Red Crossbill	+	
White-winged Crossbill	+	+*
Savannah Sparrow	+	
Dark-eyed Junco	+	
White-throated Sparrow	+	
Fox Sparrow	+	+
Swamp Sparrow	+	

Another uncommon species, the Brown Creeper (*Certhia familiaris* Linnaeus), was recorded only twice.

The Brown Creeper and the Winter Wren (*Troglodytes troglodytes* Linnaeus), two island species, were never observed on South Head during the summer of 1977. Eleven species were common to both areas. These included the Yellow-bellied Flycatcher (*Empidonax flaviventris* (Baird and Baird)), the Common Raven, Boreal Chickadee, Robin (*Turdus migratorius* Linnaeus), Gray-cheeked Thrush (*Catharus minimus* (Lafresnaye)), Blackpoll Warbler (*Dendroica striata* (Forster)), Northern Waterthrush, Pine Grosbeak (*Pinicola enucleator* Linnaeus), Pine Siskin (*Carduelis pinus* (Wilson)), White-winged Crossbill and Fox Sparrow. Fourteen mainland species were never observed on Gull Island. Six of these were the ones noted as being scarce on South Head. The other eight were more common. They included the Common Crow (*Corvus brachyrhynchos* Brehm), Black-capped Chickadee, Wilson's Warbler (*Wilsonia pusilla* (Wilson)), Red Crossbill (*Loxia curvirostra* Linnaeus), Savannah Sparrow (*Passerculus sandwichensis* (Gmelin)), Dark-eyed Junco (*Junco hyemalis* Linnaeus), White-throated Sparrow (*Zonotrichia albicollis* (Gmelin)) and Swamp Sparrow (*Melospiza georgiana* (Latham)).

One difference between the island and mainland passerine communities was the presence of a number of congeners on South Head while at Gull Island all species present were of separate genera. The South Head congeners were the following: Boreal and Black-capped Chickadees, Red and White-winged Crossbills and the Common Crow and Raven, although this latter species was only observed once at South Head. One representative from each species pair was observed on Gull Island.

Another characteristic of insular faunas is their reduced species diversity relative to the mainland (Cody 1971). Diversity indices were therefore calculated for South Head (May 18 to July 19, 1977) and Gull Island (June 16 to July 26, 1977). They are shown in Table 2. The index values ranged from 2.4388 to 4.2779 and 2.3302 to 2.8946 on the mainland and island respectively. They were found to be significantly different at the 0.005 level using a Kruskal-Wallis test, the mainland having the greater diversity.

The abundance of land birds is often greater on islands than on comparable areas of mainland (Grant 1966). This was not the case for passerines on Gull Island. Total bird densities (birds/km of transect) for each census route are shown in Table 3 for the months of June, July and the two months combined. Densities of birds did not differ between June and July on either island ($t=0.8894$, $df=9$) or mainland ($t=1.1254$, $df=20$). The mainland did, however, show a significantly higher density than Gull Island for the months of June and July combined ($t=3.4582$, $df=31$, $p < 0.01$).

The seasonal density of a bird species may change depending on their movement. Detectibility may also vary and affect the apparent density of a species. Seasonal differences in density were therefore investigated. Densities of individual bird species may be seen in Table 4. Comparisons revealed that four of the species showed no monthly differences within each area, Fox Sparrow, Pine Siskin, and the Gray-cheeked Thrush (Table 5). The Blackpoll Warbler and the Boreal Chickadee did not vary on South Head but on Gull Island were found in greater numbers in June than in July. The reverse was true for the Northern Waterthrush where

Table 2. Bird diversity indices ($\bar{d}$) for South Head, Witless Bay and Gull Island, for the months of May, June and July, 1977.

Month	$\bar{d}$ (South Head)	$\bar{d}$ (Gull Island)
	2.4388	
	2.9246	
	2.9152	
May 1977	2.4966	
	3.4261	
	2.9786	
	3.1053	
	3.4940	2.8356
	3.0461	2.8946
	3.2890	2.8744
	2.9827	2.8112
	3.1457	2.6773
	3.3224	
	3.1902	
June 1977	3.1701	
	3.1163	
	3.2841	
	3.4755	
	3.4019	
	3.5274	
	3.6511	
	3.7493	
	3.5658	2.6153
	3.8819	2.4050
	3.4348	2.3602
July 1977	3.3605	2.3302
	3.3446	2.5129
	3.4524	2.4532
	4.2779	

Table 3. Bird densities (birds/km of transect) on South Head, Witless Bay and Gull Island, for the months of June and July, 1977. (Values in brackets represent common logarithm values).

South Head		Gull Island	
June	July	June	July
40.74 (1.6100)	35.18 (1.5464)	34.72 (1.5406)	26.39(1.4214)
36.42 (1.5613)	44.44 (1.6478)	29.17 (1.4649)	31.94(1.5044)
45.06 (1.6538)	53.70 (1.7300)	19.44 (1.2888)	26.39(1.4214)
27.16 (1.4339)	40.74 (1.6100)	43.75 (1.6410)	24.31(1.3857)
27.78 (1.4437)	33.95 (1.5308)	36.11 (1.5576)	36.80(1.5659)
42.59 (1.6293)	35.80 (1.5539)		22.22(1.3468)
42.59 (1.6293)	47.53 (1.6770)		
31.48 (1.4981)			
32.72 (1.5148)			
35.18 (1.5464)			
46.30 (1.6655)			
37.04 (1.5686)			
43.21 (1.6356)			
28.40 (1.4532)			
51.85 (1.7148)			
n= 15	n= 7	n= 5	n=6
$\bar{x}$= 37.20 (1.5706)	$\bar{x}$= 41.09 (1.6137)	$\bar{x}$= 31.52(1.4986)	$\bar{x}$=27.60(1.4409)
S.D.= 1.22 (0.0872)	S.D.= 1.19 (0.0748)	S.D.= 1.36(0.1330)	S.D.=1.20(0.0806)
Total June + July		Total June + July	
n= 22		n= 11	
$\bar{x}$= 38.40 (1.5843)		$\bar{x}$= 29.32 (1.4671)	
S.D.= 1.21 (0.0843)		S.D.= 1.28 (0.1058)	

Table 4. Mean bird density values (birds/km of transect) of some common passerine species on South Head, Witless Bay and Gull Island for June, July and June + July combined, 1977. (Values in brackets represent log base 10).

Bird Species	South Head			Gull Island		
	June	July	June+July	June	July	June+July
Fox Sparrow	5.79 (.7624)	6.75 (.8295)	6.08 (.7838)	5.79 (.7627)	7.78 (.8912)	6.80 (.8328)
Robin	2.99 (.4763)	2.56 (.4080)	2.85 (.4545)	.923 (-.0348)	.99 (-.0026)	.96 (-.0158)
Northern Waterthrush	4.27 (.6305)	3.29 (.5166)	3.93 (.5943)	5.39 (.7313)	7.39 (.8685)	6.40 (.8061)
Blackpoll Warbler	6.18 (.7909)	5.61 (.7491)	6.00 (.7776)	2.48 (.3937)	.99 (-.0053)	1.50 (.1765)
Pine Siskin	4.50 (.6533)	3.80 (.5803)	4.27 (.6301)	4.43 (.6464)	2.33 (.3681)	3.12 (.4946)
Boreal Chickadee	2.28 (.3588)	1.74 (.2418)	2.14 (.3297)	6.45 (.8094)	2.57 (.4106)	3.91 (.5919)
Gray-cheeked Thrush	1.35 (.1297)	1.86 (.2706)	1.50 (.1746)	2.74 (.4381)	3.32 (.5215)	3.04 (.4836)
Black-capped Chickadee	1.46 (.1633)	1.45 (0.0605)	1.35 (.1306)			
Boreal + Black-capped Chickadees	3.25 (.5125)	2.25 (.3527)	2.92 (.4649)			

Table 5. Comparisons of bird densities (birds/km of transect) of some common species of passerines on South Head, Witless Bay and Gull Island, for the months of June, July and June + July combined, 1977, using t-test. (numbers indicate t-values). (Brackets indicate where or when bird densities are highest).

Bird Species	June vs. July		South Head vs Gull Island		
	South Head (df=20)	Gull Island (df=9)	June (df=18)	July (df=11)	June+July (df=31)
Fox Sparrow	1.5495	0.2963			1.3807
Robin	0.5738	0.4812			7.1202*** (S.H.)
Northern Waterthrush	2.2975* (June)	1.1327	1.5535	3.7648** (G.I.)	4.6512*** (G.I.)
Blackpoll Warbler	0.6285	3.6657** (June)	5.8878*** (S.H.)	7.0598*** (S.H.)	10.3396*** (S.H.)
Pine Siskin	0.5348	1.9445			1.5775
Boreal Chickadee	0.9246	2.4352* (June)	3.1938** (G.I.)	1.0958	3.5842** (G.I.)
Gray-cheeked Thrush	1.7237	1.1791			6.1004*** (G.I.)
Black-capped Chickadee	1.1527				

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

no monthly variation was noted for Gull Island but it was more abundant during June on South Head. The Black-capped Chickadee, not present on Gull Island, showed no monthly variation in density at South Head.

Number of species, species diversity and total number of birds have been shown to be lower on Gull Island than on the mainland. This should affect the density of individual species which could be reduced or increased. The density of the Fox Sparrow and Pine Siskin did not differ between the two localities (Table 5). The other species thus compared did show differences. The Robin and Blackpoll Warbler were more abundant on the mainland whereas the Northern Waterthrush, the Boreal Chickadee and the Gray-cheeked Thrush had significantly higher total summer densities on the island. No differences were detected for the Northern Waterthrush during June and the Boreal Chickadee during July.

Since the Black-capped Chickadee was only present at one site it was decided to compare it to its congener, the Boreal Chickadee, where they occur together. Its density was found to be less than the mainland Boreal Chickadee during the month of June and June and July combined, and therefore less than the Island Boreal (Table 6). No differences were observable for July. The combined values of both mainland *Parus* were compared to the lone island representative (Table 6). No difference was found for either the month of July or for June and July combined. However, there was variation for June when more chickadees were present on Gull Island. It can thus be seen that the one chickadee species on Gull Island had a density equal to or greater than the combined density of the two species on South Head.

The five most common mainland species (Blackpoll Warbler, Fox Sparrow,

Table 6. Comparisons of bird densities (birds/km of line transect) of South Head Boreal Chickadee and Black-capped Chickadee, and Gull Island Boreal Chickadee, between the months of June and July and June + July combined, 1977, using a t-test. (Numbers indicate t-values). (Brackets indicate where densities are highest).

	Mainland Boreal vs. Black-capped Chickadees	Mainland Boreal + Black-capped vs. Island Boreal Chickadees
June	2.2455* (df=28) (Boreal Chickadee)	2.2195* (df=18) (Island Boreal Chickadee)
July	1.4084 (df=12)	0.3659 (df=11)
June + July	2.7336** (df=42) (Boreal Chickadee)	1.4652 (df=31)

* $p < 0.05$

** $p < 0.01$

Pine Siskin, Northern Waterthrush and Robin) constituted 65% of the total mainland birds. The five most common island species (Fox Sparrow, Northern Waterthrush, Boreal Chickadee, Pine Siskin and Gray-cheeked Thrush) made up 86% of the total island birds. Three of the species were shared, the Fox Sparrow, Northern Waterthrush and Pine Siskin. The species dominant in only one community were the Robin and Blackpoll Warbler on the mainland (these two species had greater densities on the mainland than on Gull Island) and Boreal Chickadee and Gray-cheeked Thrush on the island (similarly these two species had greater densities on Gull Island than on South Head).

II. Structure of the vegetation

As seen above the number of bird species on Gull Island is considerably less than on South Head. Such a depleted fauna would suggest an accompanying shift in niche for some species. One such shift could occur in habitat selection. Analysis of the vegetation was therefore carried out to see if such was the case.

a) Tree density

Total tree densities for individual sampling plots are shown in Table 7. No difference was found between the areas for any of the species compared (Table 8). An equality of variance test did, however, detect differences in variance for the breeding habitat of the Fox Sparrow and the foraging habitat of the Boreal Chickadee. In the first case the variance was greater on the mainland while in the latter case the variance was higher on the island.

b) Tree composition

Five major factors in tree species composition on the bird territories

Table 7. Tree densities (# trees/.04 hectares) in breeding and foraging habitats of some bird species on South Head, Witless Bay and Gull Island, 1977. (Values in brackets represent log base 10).

Sample	Northern Waterthrush		Fox Sparrow		Boreal Chickadee		Black-capped Chickadee
no.	Gull Island	South Head	Gull Island	South Head	Gull Island	South Head	Gull Island
1	81 (1.9085)	128 (2.1072)	65 (1.8129)	228 (2.3579)	164 (2.2148)	121 (2.0828)	91 (1.9590)
2	128 (2.1072)	92 (1.9638)	46 (1.6628)	67 (1.8261)	89 (1.9494)	125 (2.0969)	125 (2.0969)
3	81 (1.9085)	72 (1.8573)	72 (1.8573)	126 (2.1004)	101 (2.0043)	72 (1.8573)	117 (2.0682)
4	72 (1.8573)	129 (2.1106)	55 (1.7404)	73 (1.8633)	59 (1.7709)	116 (2.0645)	159 (2.2014)
5	136 (2.1335)	63 (1.7993)	51 (1.7076)	38 (1.5798)	190 (2.2788)	77 (1.8865)	101 (2.0043)
6	123 (2.0899)	76 (1.8808)	69 (1.8388)	75 (1.8751)	92 (1.9638)	91 (1.9590)	102 (2.0086)
7	78 (1.8921)	71 (1.8513)		50 (1.6990)	81 (1.9085)	101 (2.0043)	204 (2.3096)
8					69 (1.8388)		90 (1.9542)
9					274 (2.4378)		
$\bar{x}$	99.86 (1.9853)	90.14 (1.9386)	59.67 (1.7700)	93.86 (1.9002)	124.33 (2.0408)	100.43 (1.9930)	123.62 (2.0628)
S.D.	27.69 (0.119)	27.62 (0.126)	10.50 (0.078)	65.30 (0.258)	71.00 (0.221)	21.27 (0.096)	39.52 (0.142)

Table 8. Comparisons of tree densities (# trees/.04 hectare) in breeding and foraging habitats of some bird species on South Head, Witless Bay and Gull Island, 1977, using t-test and equality of variance test. (Brackets indicate where variance is highest).

Bird Species	Differences in mean (t-values)	Differences in Variance (x^2 values) (df=1)
Northern Waterthrush (South Head vs. Gull Island)	0.7134 (df=12)	0.0014
Fox Sparrow (South Head vs. Gull Island)	1.1827 (df=11)	7.879** (South Head)
Boreal Chickadee (South Head vs. Gull Island)	0.5312 (df=14)	4.0102* (Island)
Boreal Chickadee vs. Black-capped Chickadee (South Head)	1.0947 (df=13)	2.1046

*$p < 0.05$

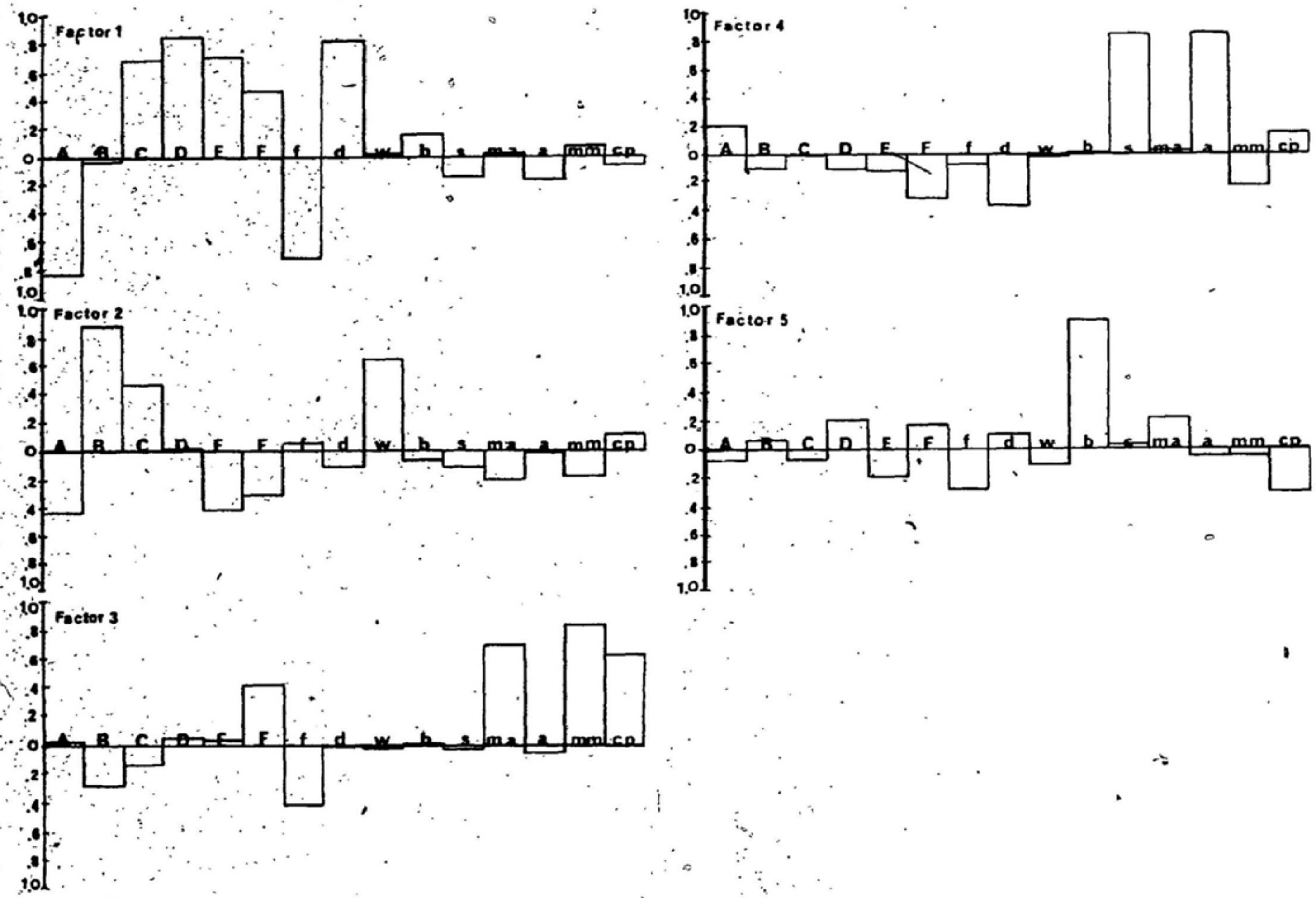
** $p < 0.005$

were isolated using factor analysis (Figure 5). The first factor (factor 1) indicates a continuum from areas of small diameter trees (class A - 2.54 cm to 7.62 cm) with a large percentage of Balsam Fir and a small number of dead trees to areas of medium diameter trees (classes C,D,E and F - 12.70 cm to 35.56 cm), many dead trees and few Balsam Fir. Factor 1 represents 30.9% of the total variance in tree species composition. Factor 2 indicates a continuum from high densities of B-diameter trees (7.62 cm to 12.70 cm) and high numbers of White Spruce to areas low in both. 18.7% of the variance is represented by this factor. The third factor (factor 3) goes from high densities of Mountain Ash, Mountain Maple and Chuckley Pear to areas with low abundance of these (9.8% of the variance). Factor 4 has a continuum from high densities of Black Spruce and Mountain Alder to areas of low density. It represents 8.8% of the total variance. The last factor (factor 5) represents 6.5% of the variance. It orders sites from ones with high densities of White Birch to areas with low densities.

The two mainland chickadee species did not differ in the tree composition of their foraging habitats (Table 9). The island population of Boreal Chickadee did, however, differ from that of the mainland for factor 4. This would be interpreted in the following way. The Boreal Chickadee habitat on Gull Island was low in Black Spruce and Mountain Alders whereas on the mainland these trees were common in areas occupied by Boreal Chickadees.

The Fox Sparrow and the Northern Waterthrush breeding habitats differed between the two localities for factor 1. On the mainland, trees were small whereas on the island intermediate to large diameter classes of trees were more prevalent. The breeding habitats on South Head also contained much

Figure 5. Factors of tree composition of breeding and foraging habitats of some bird species on South Head, Witless Bay, and Gull Island, 1977, isolated using factor analysis (A - 2.54 cm to 7.62 cm; B - 7.62 cm to 12.70 cm; C - 12.70 cm to 17.78 cm; D - 17.78 cm to 25.40 cm; E - 25.40 cm to 30.48 cm; F - 30.48 cm to 35.56 cm; f - Balsam Fir; d - Dead tree; w - White Spruce; s - Black Spruce; ma - Mountain Ash; a - Mountain Alder; mm - Mountain Maple; cp - Chuckley Pear; b - White Birch).



Factor 1
Factor 2
Factor 3
Factor 4
Factor 5
A B C D E F f d w b s ma a mm cp
1.0 .8 .6 .4 .2 0 .2 .4 .6 .8 1.0

Table 9. Comparisons of factors (from component analysis) of tree species and densities on South Head, Witless Bay and Gull Island, 1977, using t-test. (Numbers indicate t-values).

Bird Species	Factors				
	1	2	3	4	5
Northern Waterthrush					
Gull Island vs. South Head (df=12)	5.0699**	1.0825	0.2371	1.5144	0.1781
Fox Sparrow					
Gull Island vs. South Head (df=11)	5.5491**	0.2017	1.5289	1.5802	0.8839
Boreal Chickadee					
Gull Island vs. South Head (df=14)	1.4006	2.0454	0.5409	3.1042*	2.1450
Boreal Chickadee vs.					
Black-capped Chickadee South Head (df=13)	0.2914	0.3728	1.2648	0.2554	1.4850

* $p < 0.01$

**$p < 0.001$

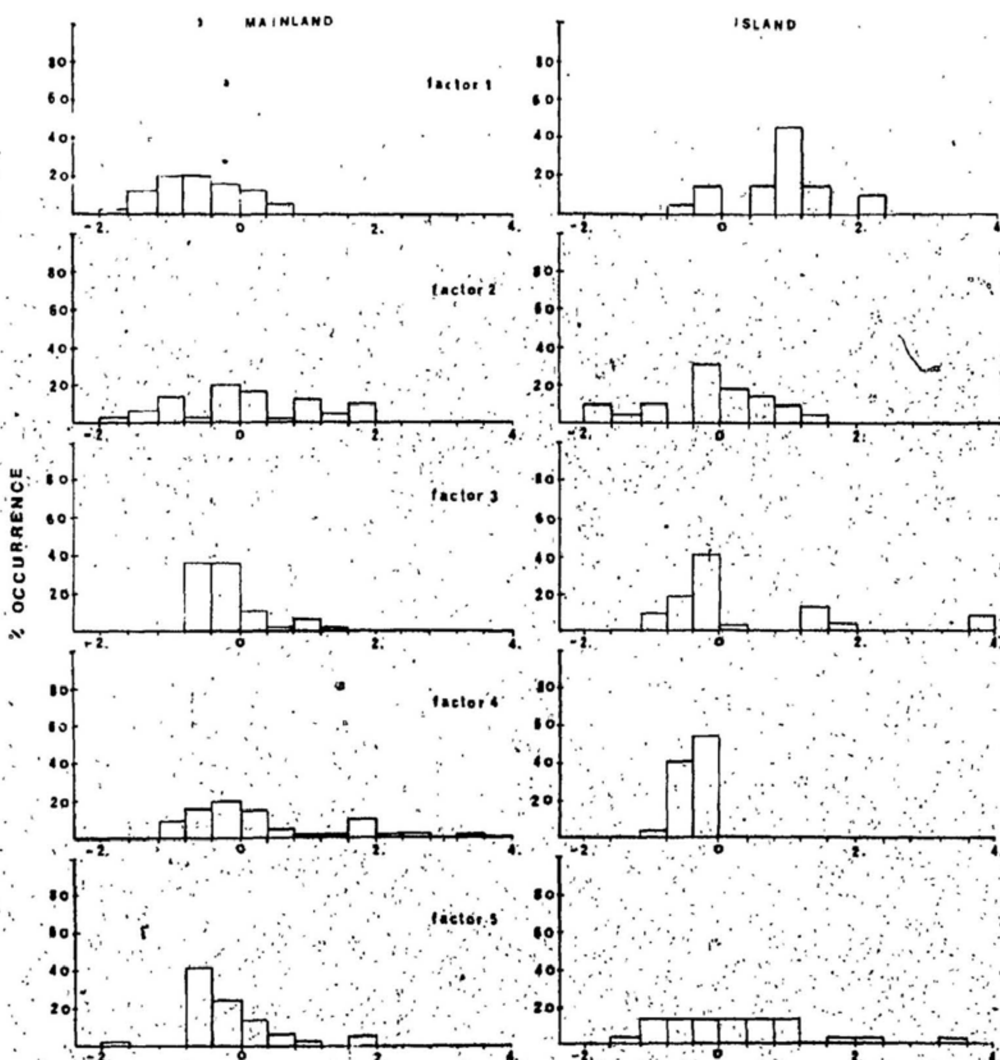
Balsam Fir and few dead trees, the former uncommon and the latter important components of the island breeding habitats of the Fox Sparrow and the Northern Waterthrush.

Differences between the island and the mainland habitats of the above species could reflect a difference in overall vegetation structure between the localities, or differences in habitat preference between the populations. To differentiate those alternatives we must compare differences in occurrence on each component of all samples from island and mainland sites.

Histograms of tree composition for Gull Island and South Head may be seen in Figure 6. A *t*-test revealed that samples of habitat characterized by factors 2,3 and 5 ($t=0.9541$; 1.3165; 1.4567; $df=49$) were equally distributed on the mainland and island. There was a significant difference for factor 1 ($t=7.709$; $df= 49$; $p < 0.001$) and factor 4 ($t= 3.3299$; $df=49$; $p < 0.01$). The mainland, therefore had greater densities of small trees (diameter of 2.54 cm to 7.62 cm), fewer dead trees, larger numbers of Balsam Fir, Black Spruce and Mountain Alder whereas the island had more intermediate to large trees (diameter of 12.70 cm to 35.56 cm), more dead trees and fewer Balsam Fir, Black Spruce and Mountain Alder.

It was seen from the above that the mainland and island habitats of the Northern Waterthrush, Fox Sparrow and Boreal Chickadee differ in tree composition for one factor each; factor 1 for the first two species and factor 4 for the third species (Table 9). Four possibilities exist to account for such differences. If the overall distribution of habitats is the same at each area, the species are showing different preferences at each locality. If the overall distribution of habitats differs between the

Figure 6. Tree composition (using values of all bird species) of South Head, Witless Bay and Gull Island, 1977, using factor analysis.


MAINLAND
ISLAND
factor 1
factor 2
factor 3
factor 4
factor 5
% OCCURRENCE
80
60
40
20
-2.
0
2.
4.

areas three relationships are possible. The birds may choose the same relative position on the habitat continuum represented by the factor, but the habitats still differ in absolute properties because of their differential occurrence. The birds may show a preference for habitats with the same absolute properties, but the occurrence of such similar habitats differsbetween the localities. Finally, the birds may show habitat displacement or expansion, occupying habitats differing in both relative and absolute properties between the two sites. The factors where differences were observed are not evenly distributed on the island and mainland, as seen above. A t-test of the deviation from the overall means revealed that there was no significant difference for the Fox Sparrow in factor 1 ($t= 0.8592$; $df= 11$), Northern Waterthrush in factor 1 ($t= 1.3107$; $df=12$) and for the Boreal Chickadee (factor 4) ($t= 0.2607$; $df= 14$). Therefore each species is choosing similarly along the available habitat gradients. The relative preference of each species has not altered from mainland to island, but the range of choice of habitats has changed.

c) Shrub density

Total shrub densities for individual sampling plots are shown in Table 10. Analysis, using a t-test, revealed no significant difference between the foraging habitats of mainland chickadee species ($t=2.160$; $df= 13$). Differences were detected in mainland and island Boreal Chickadee foraging habitats ($t= 2.624$; $df=14$; $p < 0.02$) and breeding habitats of mainland and island Fox Sparrow ($t= 3.106$; $df= 11$; $p < 0.01$) and Northern Waterthrush ($t= 3.055$; $df= 12$; $p < 0.05$). In all cases the higher shrub densities were found on South Head.

Table 10. Shrub densities (#shrubs/.04 hectare) in breeding and foraging habitats of some bird species on South Head, Witless Bay and Gull Island, 1977. (Values in brackets represent log base 10).

Sample no.	Northern Waterthrush		Fox Sparrow		Boreal Chickadee		Black-capped Chickadee
	South Head	Gull Island	South Head	Gull Island	South Head	Gull Island	South Head
1	79 (1.8976)	4 (0.6021)	77 (1.8865)	40 (1.6021)	22 (1.3424)	26 (1.4150)	31 (1.4914)
2	39 (1.5911)	7 (.8451)	47 (1.6721)	29 (1.4624)	38 (1.5798)	8 (0.9031)	38 (1.5798)
3	36 (1.5563)	1 (0)	52 (1.7160)	27 (1.4314)	36 (1.5563)	5 (0.6990)	55 (1.7404)
4	51 (1.7076)	16 (1.2041)	58 (1.7634)	18 (1.2553)	51 (1.7076)	34 (1.5315)	27 (1.4314)
5	35 (1.5441)	27 (1.4314)	46 (1.6628)	44 (1.6435)	84 (1.9243)	19 (1.2788)	63 (1.7993)
6	65 (1.8129)	2 (0.3010)	39 (1.5911)	26 (1.4150)	65 (1.8129)	28 (1.4472)	44 (1.6435)
7	59 (1.7709)	38 (1.5798)	56 (1.7482)		31 (1.4914)	31 (1.4914)	27 (1.4314)
8						1 (0)	53 (1.7243)
9						29 (1.4624)	
$\bar{x}$	52.0 (1.6972)	13.57 (0.8519)	53.57 (1.7200)	30.67 (1.4583)	46.71 (1.6307)	20.11 (1.1032)	42.25 (1.6052)
S.D.	16.64 (0.137)	14.20 (0.589)	12.18 (0.094)	9.63 (0.143)	21.37 (0.198)	12.39 (0.501)	13.74 (1.44)

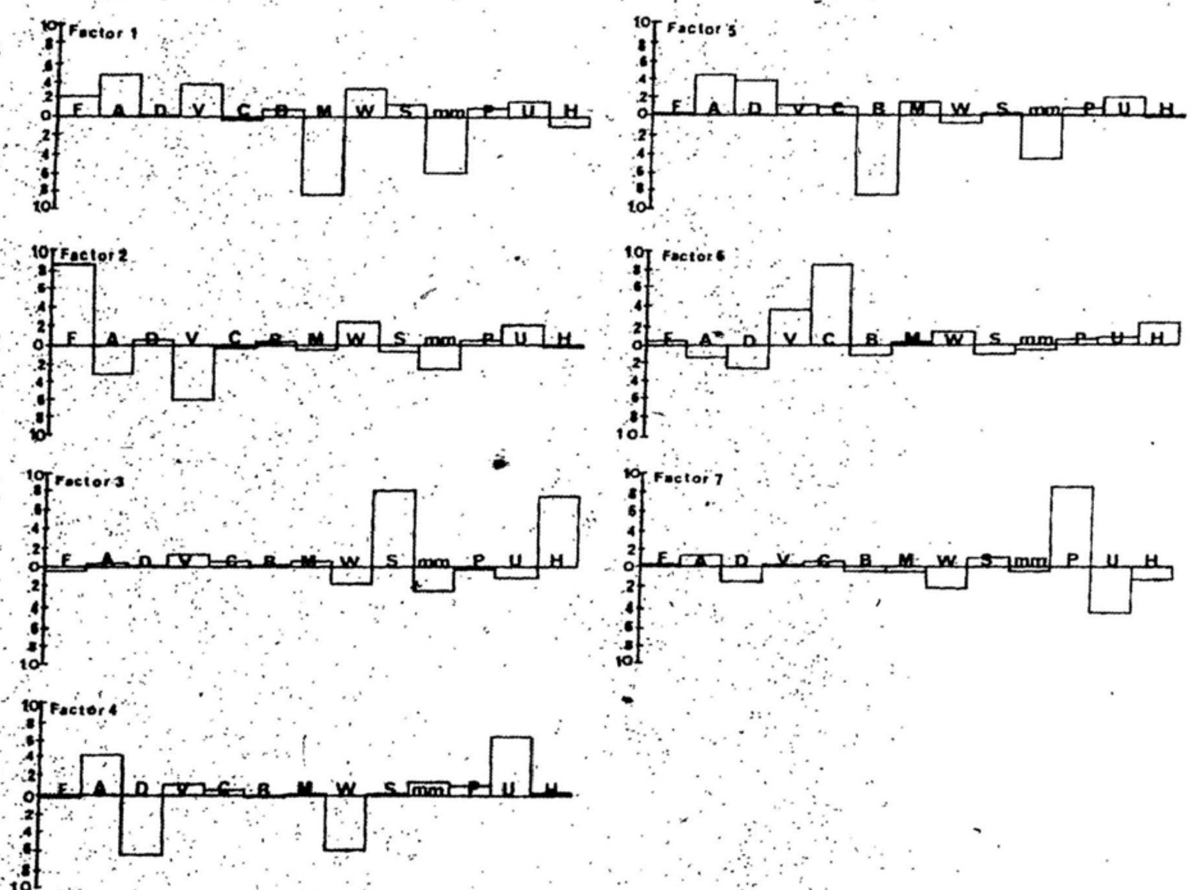
d) Shrub composition

In the case of shrub composition seven factors were present (Figure 7). They can be interpreted as follows: Factor 1 - areas high in Mountain Ash and Mountain Maple to areas with low densities of these species. It represents 16.2% of the total variance. Factor 2 - areas low in Balsam Fir and high in Northern Wild Raisin to areas high in Balsam Fir and Northern Wild Raisin (14.6% of the total variance). Factor 3 - areas low in Black Spruce and Mountain Holly to areas high in these species (10.8% of the variance). Factor 4 - high in dead shrubs and White Spruce and low in one unidentified deciduous species to areas low in dead shrubs and White Spruce and high in the unknown species (9.1% of the variance). Factor 5 - high in White Birch to low in birch (8.4% of the variance). Factor 6 - low in Chuckley Pear to high in Chuckley Pear (7.9% of the variance). Factor 7 - low in Pin Cherry to high in Pin Cherry (7.7% of the variance).

Results of the comparisons of each of these factors can be seen in Table 11. No difference was observed for chickadees (Boreal Chickadee, South Head vs. Gull Island, and Boreal Chickadee vs. Black-capped Chickadee on South Head). Similarly there was no difference in the Northern Waterthrush breeding habitats. Two factors differed in the Fox Sparrow habitat, however, factors 1 and 5. To interpret this the South Head population is exploiting areas low in Mountain Ash, Moutain Maple, White Birch, whereas these shrub species were abundant on Fox Sparrow localities on Gull Island.

Differences in shrub composition of selected habitats between island and mainland could be merely due to overall differences in the vegetation structure of each area. By comparing the occurrence of each component of all

Figure 7. Factors of shrub composition of breeding and foraging habitats of some bird species on South Head, Witless Bay and Gull Island, 1977, isolated using factor analysis. (F - Balsam Fir; A - Mountain Alder; D - dead tree; V - Northern Wild Raisin; C - Chuckley Pear; B - White Birch; M - Mountain Ash; W - White Spruce; S - Black Spruce; mm - Mountain Maple; P - Pin Cherry; U - unknown; H - Mountain Holly).



Factor 1
Factor 2
Factor 3
Factor 4
Factor 5
Factor 6
Factor 7
F A D V C B M W S mm P U H
10 8 6 4 2 0 2 4 6 8 10

Table 11. Comparisons of factors (from component analysis) of shrub species on South Head, Witless Bay and Gull Island, 1977, using a t-test. (Numbers indicate t-values).

Bird Species	Factors 1	2	3	4	5	6	7
Northern Waterthrush (Gull Island vs. South Head) (df=12)	1.3703	1.3872	1.6237	0.5766	1.3121	0.8515	1.3683
Fox Sparrow (Gull Island vs. South Head) (df=11)	2.9026*	0.9750	0.5414	1.5132	4.1965**	0.3369	0.0426
Boreal Chickadee (Gull Island vs. South Head) (df=14)	1.9163	0.1494	1.5639	0.7329	0.3830	0.4375	0.7785
Boreal Chickadee vs. Black-capped Chickadee (South Head) (df=13)	0.4398	0.0040	0.8054	0.7936	0.9849	0.2337	0.1928

* $p < 0.02$

** $p < 0.01$

samples, factor by factor, differences can be detected.

The distribution of each factor of shrub composition can be seen in Figure 8. Analysis, using a t-test, revealed no significant difference for factor 2 ($t= 0.1971$; $df= 49$), factor 6 ($t= 0.3107$; $df= 49$) and factor 7 ($t= 1.2349$; $df=49$). Differences between the island and mainland shrub composition were seen in factor 1 ($t= 4.1819$; $df= 49$; $p < 0.001$), factor 3 ($t= 2.1528$; $df=49$; $p < 0.05$) and factor 5 ($t= 3.1773$; $df=49$; $p < 0.02$). This can be interpreted in the following way. Gull Island had high densities of Mountain Ash, Mountain Maple and White Birch and low numbers of Black Spruce and Mountain Holly, relative to the mainland where densities of Mountain Ash, Mountain Maple and White Birch were low and densities of Black Spruce and Mountain Holly were high.

The shrub composition differed between the island and mainland habitats for the Fox Sparrow, for factors 1 and 5. These two factors were, however, not similarly distributed at each locality. A t-test revealed that there was no difference in the distribution around the overall mean for factor 1 ($t= 0.7875$; $df=11$). Differences were detected for the island Fox Sparrow for factor 5 ($t= 2.1320$; $df=11$; $p < 0.05$). On the island the Fox Sparrow is selecting one end of the available habitat continuum whereas on the mainland the preference is for the opposite end of the habitat gradient. This indicates a shift in habitat selection from areas on the mainland with low densities of White Birch to areas with high densities of White Birch on the island.

e) Canopy and ground cover

The results obtained for canopy and ground cover can be seen in Tables 12 and 13. There was no difference in the canopy cover (using

Figure 8. Shrub composition (using values of all bird species) of South Head, Witless Bay and Gull Island, 1977, isolated using factor analysis.

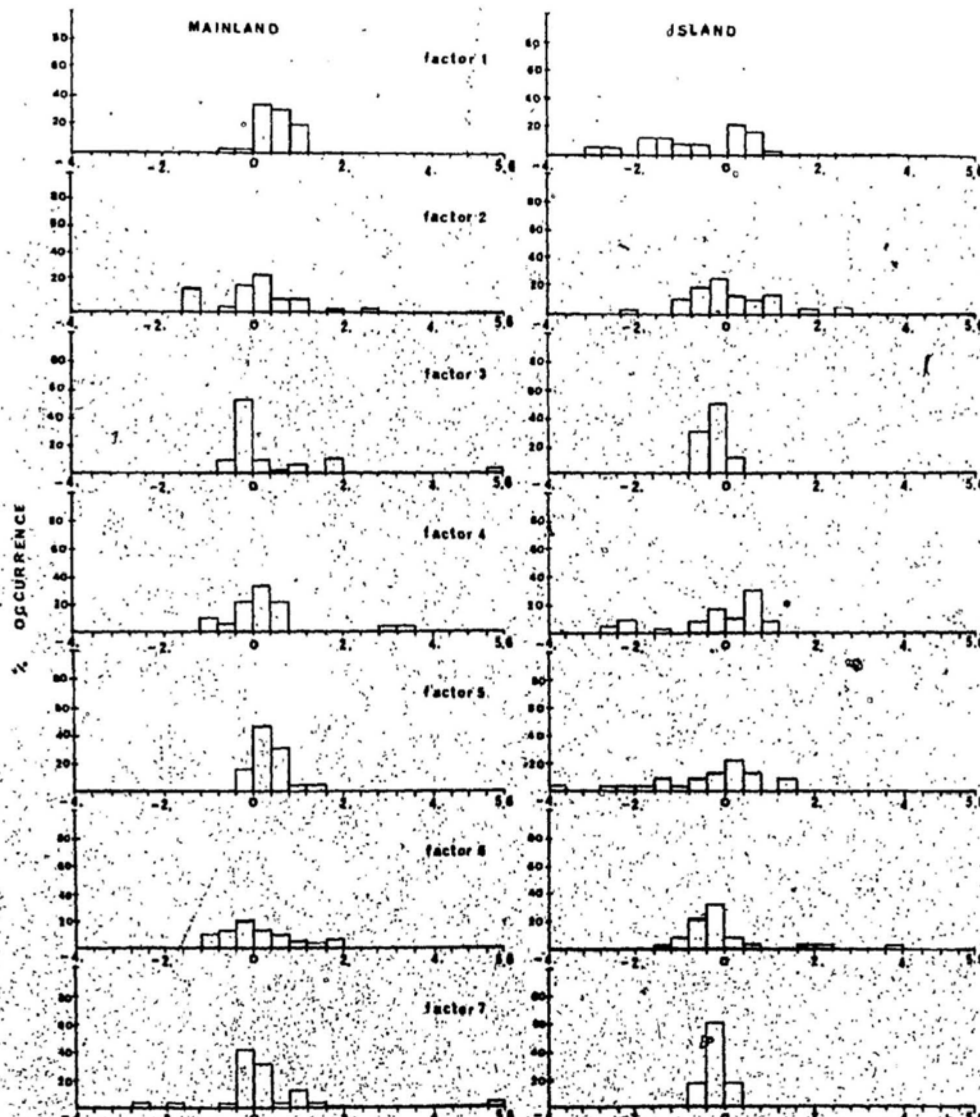

MAINLAND
ISLAND
factor 1
factor 2
factor 3
factor 4
factor 5
factor 6
factor 7
% OCCURRENCE
-4.
-2.
0
2.
4.
5.6
20
40
60
80

Table 12. Number of plus (+) readings of canopy cover (out of 20)* in breeding and foraging habitats of some bird species on South Head, Witless Bay and Gull Island, 1977.

Sample	Fox Sparrow		Northern Waterthrush		Boreal Chickadee		Black-capped Chickadee
no.	Gull Island	South Head	Gull Island	South Head	Gull Island	South Head	South Head
1	10+	15+	8+	8.57+	14+	10+	9+
2	6+	11+	8+	18+	12+	16.19+	17.14+
3	5+	14+	4+	13+	14+	13+	4+
4	4.21+	13.68+	9+	7+	13+	14+	15+
5	5+	12+	7.37+	13+	14+	12+	16+
6	10+	12+	9+	10+	16+	16+	14+
7		7+	15+	8+	12+	9+	18.10+
8					4+		14+
9					10+		

*(Where more or less than 20 readings were taken the values were scaled to a total of 20).

Table 13. Number of plus (+) readings of ground cover (out of 20)* in breeding and foraging habitats of some bird species on South Head, Witless Bay and Gull Island, 1977.

Sample no.	Fox Sparrow		Northern Waterthrush		Boreal Chickadee		Black-capped Chickadee
	Gull Island	South Head	Gull Island	South Head	Gull Island	South Head	South Head
1	14+	6+	15.24+	9.52+	12+	11+	11+
2	15+	15+	17+	9+	12+	10.48+	10.48+
3	16+	9+	13+	13+	13+	13+	12+
4	16+	14+	15+	10+	16+	12+	9+
5	17+	13+	14.74+	12+	4.21+	13+	7+
6	14.74+	11+	16+	12+	4+	7+	6+
7		16.19+	15+	12+	13+	11+	6.67+
8					13+		9.52+
9					14.74+		

* (Where more or less than 20 readings were taken the values were scaled to a total of 20).

Kruskal-Wallis test) of the island and mainland Boreal Chickadee ($H = 0.072$; $df = 1$) and Northern Waterthrush ($H = 1.99$; $df = 1$). Similarly no difference was observed between the mainland Boreal and Black-capped Chickadees ($H = 0.48$; $df = 1$). The canopy was significantly more open on Gull Island for the Fox Sparrow ($H = 7.44$; $df = 1$; $p < 0.01$) habitat than it was on the mainland.

There was no difference in the ground cover of the chickadees (Boreal vs. Black-capped, mainland ($H = 3.69$; $df = 1$) and Boreal Chickadee, island vs. mainland ($H = 1.053$; $df = 1$))or the Fox Sparrow ($H = 3.48$; $df = 1$). Ground cover was greater on the mainland in the case of the Northern Waterthrush breeding habitat ($H = 9.49$; $df = 1$; $p < 0.005$).

Table 14 lists the two or three commonest plant species comprising the ground cover. Ground cover on the mainland, in the Fox Sparrow habitat, consisted chiefly of Crackerberry (*Cornus canadensis* Linnaeus), Blueberry (*Vaccinium* sp.) with occasional moss or Labrador tea (*Ledum groenlandicum* Oeder). The vegetation was relatively low, a few inches in the case of Crackerberry and moss, and where heaths were found, compact shrubs were present. On the island, ground vegetation was knee-deep or higher and not as compact as the heaths growing on the mainland. The main species were Skunk Currant (*Ribes glandulosum* Grauer), Red Raspberry (*Rubus idaeus* Linnaeus) and Spinulose Woodfern (*Dryopteris spinulosa* (O.F.Mueller) Watt).

The ground cover vegetation of the Northern Waterthrush was quite similar to that of the Fox Sparrow. Crackerberry and Blueberry were again the dominant mainland types. Also present were Labrador Tea and moss with Spinulose Woodfern, Partridgeberry (*Vaccinium vitis-idaea*

Table 14. Ground vegetation in breeding and foraging habitats of some bird species on South Head, Witless Bay and Gull Island, 1977. Plant species are listed in order of abundance.

Sample	Fox Sparrow		Northern Waterthrush		Boreal Chickadee		Black-capped Chickadee
no.	South Head	Gull Island	South Head	Gull Island	South Head	Gull Island	South Head
1	Crackerb. Moss Blueb.	S. Cur. Raspb.	Crackerb. Lab. Tea	Fern Raspb. S. Cur.	Blueb.	Raspb. S. Cur. Moss	Blueb.
2	Crackerb. Blueb.	Fern S. Cur.	Crackerb. Moss	Fern S. Cur.	Moss Grass Crackerb.	S. Sor. Grass Fern	Moss Grass Crackerb.
3	Crackerb. Moss	Fern S. Cur. Raspb.	Crackerb. Moss Fern	Fern Raspb. S. Sor.	Crackerb. Moss Fern	Crackerb. Raspb. Fern	Blueb. Partridge. Crackerb.
4	Crackerb. Blueb.	Raspb. S. Cur.	Fern Moss Lab. Tea	Fern S. Cur.	Crackerb. Moss Blueb.	Fern Crackerb.	Crackerb. Partridge. Blueb.
5	Crackerb. Blueb. Lab. Tea	S. Cur. Raspb.	Crackerb. Partridge.	S. Cur.	Crackerb. Blueb. Partridge.	Moss Fern	Crackerb. Blueb. Moss
6	Crackerb. Blueb.	Fern S. Cur. Raspb.	Crackerb. Blueb.	S. Cur. Fern	Crackerb. Blueb. Moss	Moss Twin f.	Crackerb. Moss
7	Blueb. Crackerb.		Bakeap. Crackerb.	Raspb. S. Cur. Fern	Blueb.	Fern S. Cur.	Moss Crackerb.
8						Fern Raspb. S. Sor.	Crackerb. Blueb.
9						Fern S. Cur. Raspb.	

Bakea. - Bakeapple; Lab. Tea - Babrador Tea; S. Cur. - Skunk Currant

Blueb. - Blueberry; Partridge. - Partridgeberry; S. Sor. - Sheep Sorrel

Crackerb. - Crackerberry; Raspb. - Raspberry; Twin f. - Twin Flower

Loddiges) and Bakeapple (*Rubus chamaemorus* Linnaeus). There were still two levels, low lying herbs on the ground and low shrubbery. On the island Skunk Currant, Raspberry and Spinulose Woodfern were still dominant. To this relatively tall layer of ground cover was added lower growing Sheep Sorrel (*Rumex acetosella* Linnaeus).

Data on the mainland Chickadees (Boreal and Black-capped) showed a similarity in the ground cover, composed of Crackerberry and moss with occasional Partridgeberry and grass. Fern was found once. On the island fern was dominant along with Skunk Currant and Raspberry. Moss was associated with ground cover as was Sheep Sorrel and Twin flower (*Linnaea borealis* Linnaeus). Grass was noted. There were therefore three "layers" on the island chickadee habitat; the high growing ferns, currants and raspberry, the lower growing Sheep Sorrel and the ground layer of moss and Twin flower.

f) Maximum tree height

There was no significant difference in the tree height (Table 15). The confidence limits are plotted in Figure 9. Tree heights in Chickadee habitats were quite similar, the two mainland species being almost identical. The Fox Sparrow did differ in the size of these limits. There was a difference in variance between the island and mainland populations ($x^2 = 5.9407$; df = 1; $p < 0.025$). The Fox Sparrow on Gull Island was exploiting a much greater range of tree heights. No difference was detected for the Northern Waterthrush ($x^2 = 0.2080$).

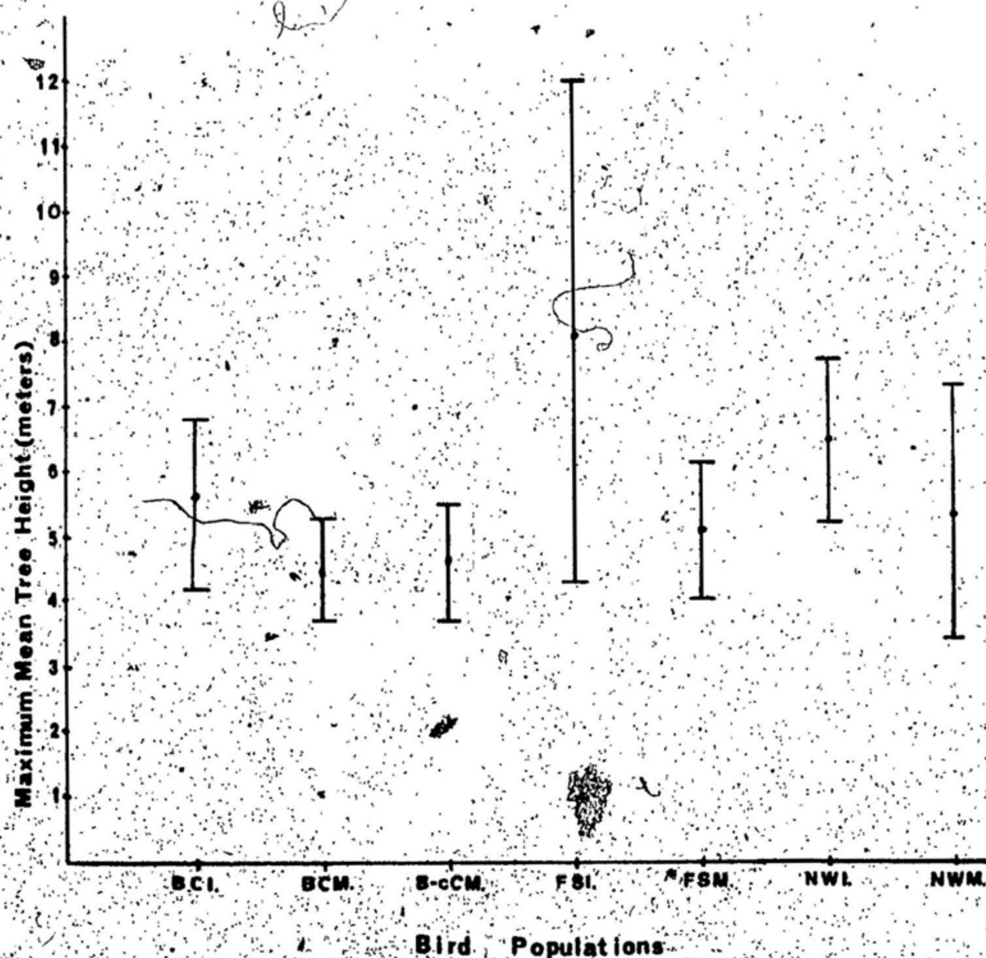
g) Other features

One feature of the Northern Waterthrush breeding habitat was the presence or absence of water within or in close proximity to the sampling

Table 15. Maximum mean tree heights and confidence limits in breeding and foraging habitats of some bird species on South Head, Witless Bay and Gull Island, 1977.

Bird Species	Locality	Mean ($\bar{x}$) (meters)	Confidence Limits
Boreal Chickadee	Gull Island	5.51	4.20 → 6.82 (± 1.31)
Boreal Chickadee	South Head	4.49	3.70 → 5.28 (± 0.79)
Black-capped Chickadee	South Head	4.61	3.72 → 5.50 (± 0.89)
Fox Sparrow	Gull Island	8.15	4.26 → 12.04 (± 3.89)
Fox Sparrow	South Head	5.08	4.01 → 6.15 (± 1.07)
Northern Waterthrush	Gull Island	6.47	5.20 → 7.74 (± 1.27)
Northern Waterthrush	South Head	5.36	3.41 → 7.31 (± 1.95)

Figure 9. Confidence intervals for maximum mean tree height of breeding and foraging habitats of some bird species on South Head, Witless Bay and Gull Island, 1977. (BCI - Boreal Chickadee, island; BCM - Boreal Chickadee, mainland; B-cCM - Black-capped Chickadee, mainland; FSI - Fox Sparrow, island; FSM - Fox Sparrow, mainland; NWI - Northern Waterthrush, island; NWM - Northern Waterthrush, mainland).



Maximum Mean Tree Height (meters)
12
11
10
9
8
7
6
5
4
3
2
1
B.C.I.
BCM.
B-cCM.
FSI.
FSM.
NWI.
NWM.
Bird Populations

plots. Water, either still or flowing, was always found in association with mainland habitats. Of the seven samples taken on Gull Island only one had water present within the area.

h) Summary of vegetation structure

Table 16 summarizes the results of the vegetation structure. It becomes obvious at first glance that the Boreal Chickadee and the Black-capped Chickadee on South Head are exploiting a similar habitat. The mainland and island Boreal populations vary in a number of aspects, including tree composition, shrub composition, ground vegetation and range of tree density.

The Northern Waterthrush occupied areas similar in vegetation structure except for ground cover and tree density. There was a significant difference in ground cover but no difference in tree density variance. Most notable was the absence of water within island habitats.

Island and mainland Fox Sparrow habitats differ from each other in all aspects investigated except ground cover. Tree density and maximum tree height, however, differed only in variance. Fox Sparrows showed the most variance in vegetation structure.

III. Foraging behavior

A shift in niche can occur through changes in habitat use, hence the reason for studying vegetation structure in the preceding section. Additionally, changes in foraging behavior can parallel or occur independently of changes in habitat use. Only one species of chickadee was present on Gull Island whereas two species were relatively abundant on the mainland. The chickadees therefore were chosen for investigation of

Table 16. Summary of the results of the vegetation structure of breeding and foraging habitats of some bird species on South Head, Witless Bay and Gull Island, 1977. ((-) not significantly different; (+) significantly different)

	Fox Sparrow (South Head vs. Gull Island)	Northern Waterthrush (South Head vs. Gull Island)	Boreal Chickadee (South Head vs. Gull Island)	Black-capped Chickadee (South Head)
Tree Density	−	−	−	−
Variance	+	−	+	−
Tree Composition	+	+	+	−
Shrub Density	+	+	+	−
Shrub Composition	+	−	−	−
Canopy Cover	+	−	−	−
Ground Cover	−	+	−	−
Ground Vegetation	+	+	+	−
Maximum Tree Height	−	−	−	−
Variance	+	−	−	−
Presence of Water		+		

foraging differences interspecifically within localities and intra-specifically between localities. The two mainland *Parus* species were seen to exploit a similar habitat (Table 16). One would therefore expect ecological isolation through differences in their foraging behavior. Where only one species is present (Gull Island) one might predict a broadening of the foraging niche (Crowell 1962).

The results of foraging behavior of the three chickadee populations can be seen in Table 17 (a,b,c). Boreal Chickadees on the island and mainland showed significant differences as did the two mainland groups (Table 18). Figure 10 (a,b,c) illustrates where the differences occur. Although overlap is seen, trends in foraging behavior can be detected.

a) Foraging height

Boreal Chickadees on Gull Island foraged relatively little at low heights, but concentrated their time between 1.52 m and 6.10 m (figure 10a). They were also observed relatively more above 6.10 m than at 0.30 m or below. The mainland counterpart foraged at lower heights, showing a peak between 1.52 m and 3.05 m. They were observed more at lower levels than above 6.10 m. The Black-capped Chickadee exploited lower heights than its congener. It was never observed above 6.10 m and showed a peak between 0.30 m and 1.52 m. These foraging height differences existed even though tree height did not differ between the foraging habitats of each population (Figure 7).

b) Vegetation type

None of the three groups exploited live deciduous trees or shrubs to the extent that live evergreen and non-green vegetation were used (Figure 10b). Both the island Boreal and the mainland Black-capped Chickadees

Table 17 a. Time spent foraging (in seconds) at different heights by chickadees on South Head, Witless Bay and Gull Island, during the summer of 1977.

BOREAL CHICKADEE (South Head)	June 9 - 20	June 21 - July 20	June 9 - Aug. 9
Ground	73	34	107
Ground ≤ .3m	14	55	74
.3 m ≤ 1.5 m	179	331	656
1.5 m ≤ 3.05m	525	915	1757
3.05m ≤ 6.1 m	216	455	704
>6.1 m	0	59	59
BOREAL CHICKADEE (Gull Island)			
Ground	6	5	11
Ground ≤ .3m	14	6	20
.3 m ≤ 1.5 m	150	220	411
1.5 m ≤ 3.05m	652	938	1682
3.05m ≤ 6.1 m	682	726	1408
>6.1 m	61	266	327
BLACK-CAPPED CHICKADEE (South Head)			
Ground	25	159	184
Ground ≤ .3 m	65	420	485
.3 m ≤ 1.5 m	134	1336	1665
1.5 m ≤ 3.05m	125	1212	1436
3.05m ≤ 6.1 m	0	184	184
>6.1 m	0	0	0

Table 17 b. Time spent foraging (in seconds) in different types of vegetation by chickadees on South Head, Witless Bay and Gull Island, during the summer of 1977.

BOREAL CHICKADEE. (South Head)	June 9 - 20	June 21 - July 20	June 9 - Aug.9
Deciduous	59	86	160
Live Evergreen Vegetation	619	1319	2270
Non-green Vegetation	218	331	735
BOREAL CHICKADEE (Gull Island)			
Deciduous	181	124	305
Live Evergreen Vegetation	265	685	1009
Non-green Vegetation	1113	1364	2551
BLACK-CAPPED CHICKADEE (South Head)			
Deciduous	115	540	673
Live Evergreen Vegetation	5	244	291
Non-green Vegetation	186	2332	2752

Table 17 c. Time spent foraging (in seconds) on different parts of the tree, by chickadees on South Head, Witless Bay and Gull Island, during the summer of 1977.

BOREAL CHICKADEE (South Head)	June 9 - 20	June 21 - July 20	June 9 - Aug. 9
Trunk	11	10	75
Center	164	270	525
Middle	108	619	876
Outer	441	741	1402
BOREAL CHICKADEE (Gull Island)			
Trunk	297	362	669
Center	340	478	845
Middle	347	548	958
Outer	299	656	988
BLACK-CAPPED CHICKADEE (South Head)			
Trunk	44	172	231
Center	60	1035	1227
Middle	46	986	1084
Outer	5	324	404

Table 18. Differences in foraging behavior in chickadees on South Head, Witless Bay and Gull Island, during the summer of 1977, using G-test. (Numbers represent G-values).

	Boreal Chickadee (South Head vs. Gull Island)	Boreal vs. Black-capped Chickadees (South Head)
Foraging Height (df = 5)	591.10*	1208.33*
Vegetation Type (df = 2)	1536.02*	3274.97*
Part of Tree Used (df = 3)	642.92*	977.74*

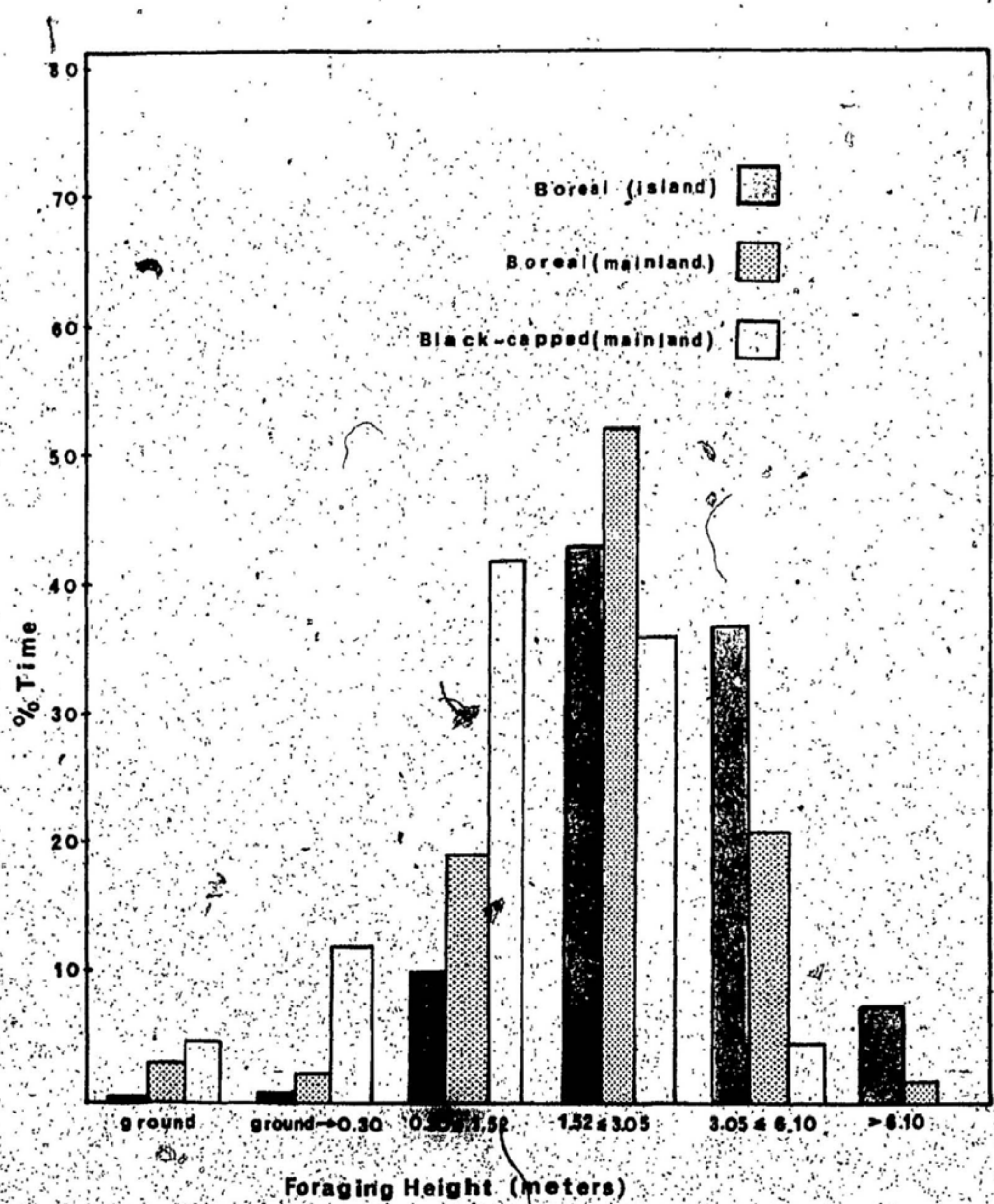
* $p < 0.005$

Figure 10. Foraging behavior of Boreal and Black-capped Chickadees on South Head, Witless Bay and Gull Island, during the summer (June 9 - Aug. 9) of 1977.

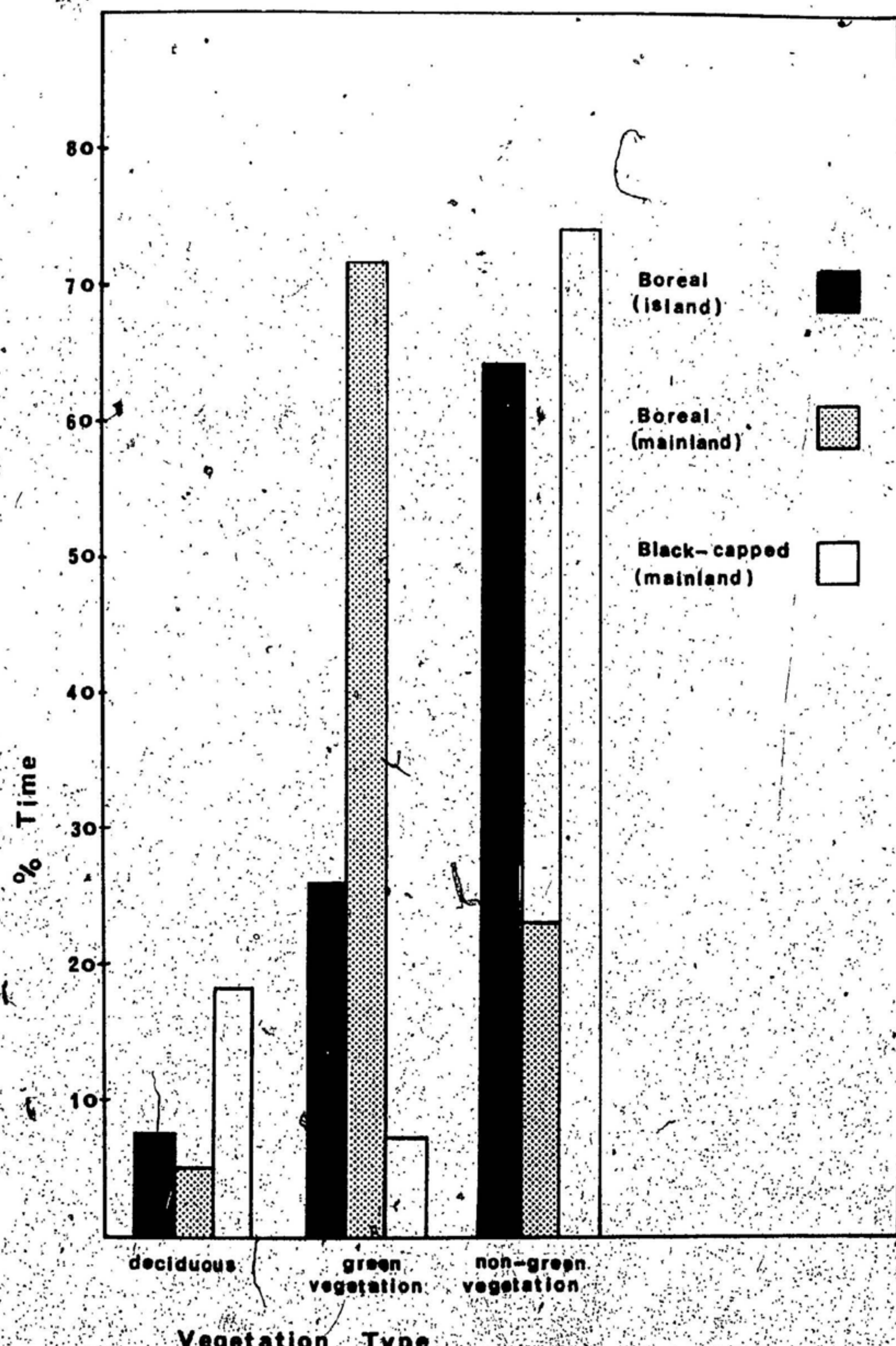
a) Foraging height

b) Vegetation type

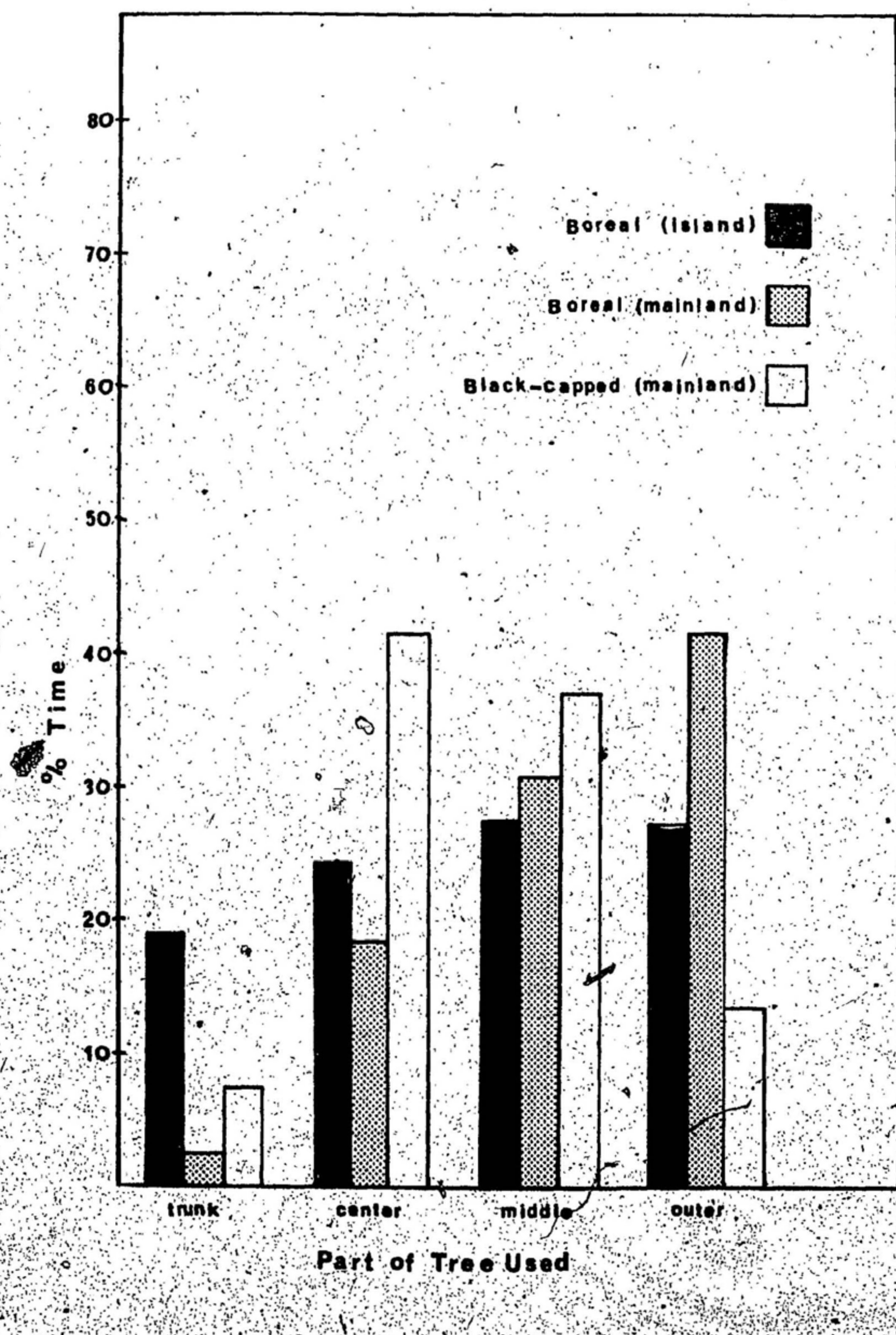
c) Part of tree used



80
70
60
50
40
30
20
10
% Time
Boreal (island)
Boreal (mainland)
Black-capped (mainland)
ground
ground→0.30
1.52 ≤ 3.05
3.05 ≤ 6.10
>6.10
Foraging Height (meters)



80
70
60
50
40
30
20
10
% Time
Boreal (island)
Boreal (mainland)
Black-capped (mainland)
deciduous
green vegetation
non-green vegetation
Vegetation Type



80
70
60
50
40
30
20
10
% Time
Boreal (island)
Boreal (mainland)
Black-capped (mainland)
trunk
center
middle
outer
Part of Tree Used

concentrated their efforts on vegetation lacking green foliage. The next highest preference was for live evergreen by the island Boreal Chickadee whereas the Black-capped Chickadee preferred deciduous vegetation to live evergreen. Mainland Boreal Chickadees spent the majority of their time on green needles. Like its island counterpart it spent the least amount of time on deciduous vegetation.

c) Part of the tree used

The Gull Island Boreal Chickadees did not appear to prefer any particular area on the tree but distributed themselves more or less evenly from the trunk to the outer branches (Figure 10c). The behavior of the chickadees on South Head was different. Here the Boreal Chickadees spent the majority of their time on the periphery of the trees. The Black-capped Chickadees on the other hand, were usually found more towards the center.

d) Seasonal differences

Seasonal differences in foraging behavior were observed within each population on South Head and Gull Island (Table 17 a,b,c and 19). This was true of foraging height, vegetation type and the part of the tree used (Figure 11 a,b,c). Each population tended to forage somewhat higher during the second part of the summer (June 21 - July 20). Foraging on deciduous trees decreased and on green vegetation increased during this period for all three populations. The Boreal Chickadees, on both island and mainland decreased their time spent on non-green vegetation whereas the Black-capped Chickadees increased their foraging frequency in this vegetation type during the second half of the summer. The island Boreal Chickadee tended to forage more towards the outer end of the branches in the second half of the summer and less on the trunk. The same was true of the Black-capped

Table 19. Seasonal variations in foraging behavior within chickadee populations on South Head, Witless Bay and Gull Island, 1977, using G-test. (Numbers indicate G-values).

	Boreal Chickadee (South Head) (June 9 - 20 vs. June 21 - July 20)	Boreal Chickadee (Gull Island) (June 9 - 20 vs. June 21 - July 20)	Black-capped Chickadee (South Head) (June 9 - 20 vs. June 21 - July 20)
Foraging Height (df = 5)	110.402*	1838.56*	47.936*
Vegetation Type (df = 2)	14.296*	1885.852*	76.712*
Part of Tree Used (df = 3)	135.662*	36.478*	71.042*

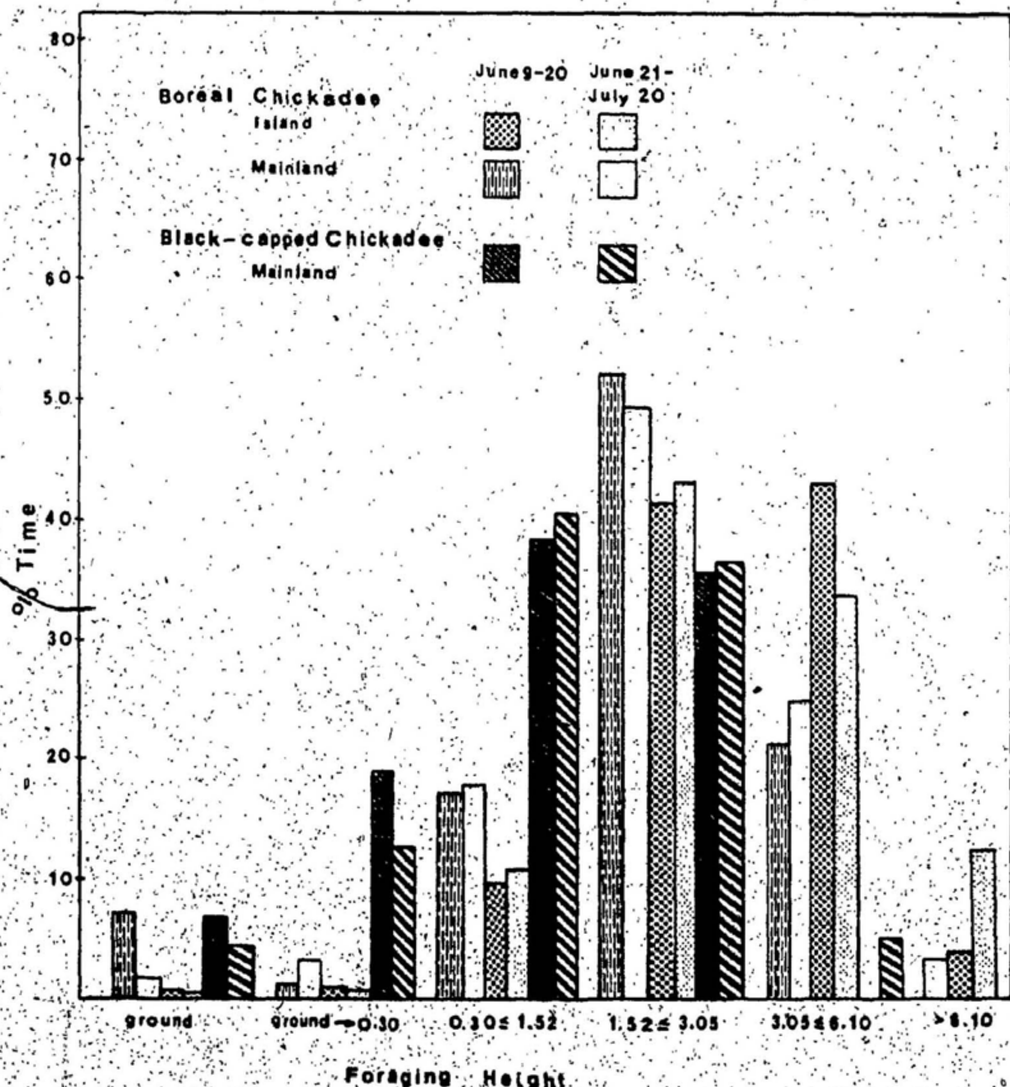
* $p < 0.005$

Figure 11. Foraging behavior of Boreal and Black-capped Chickadees on South Head, Witless Bay and Gull Island, during the summer of 1977, showing seasonal differences.

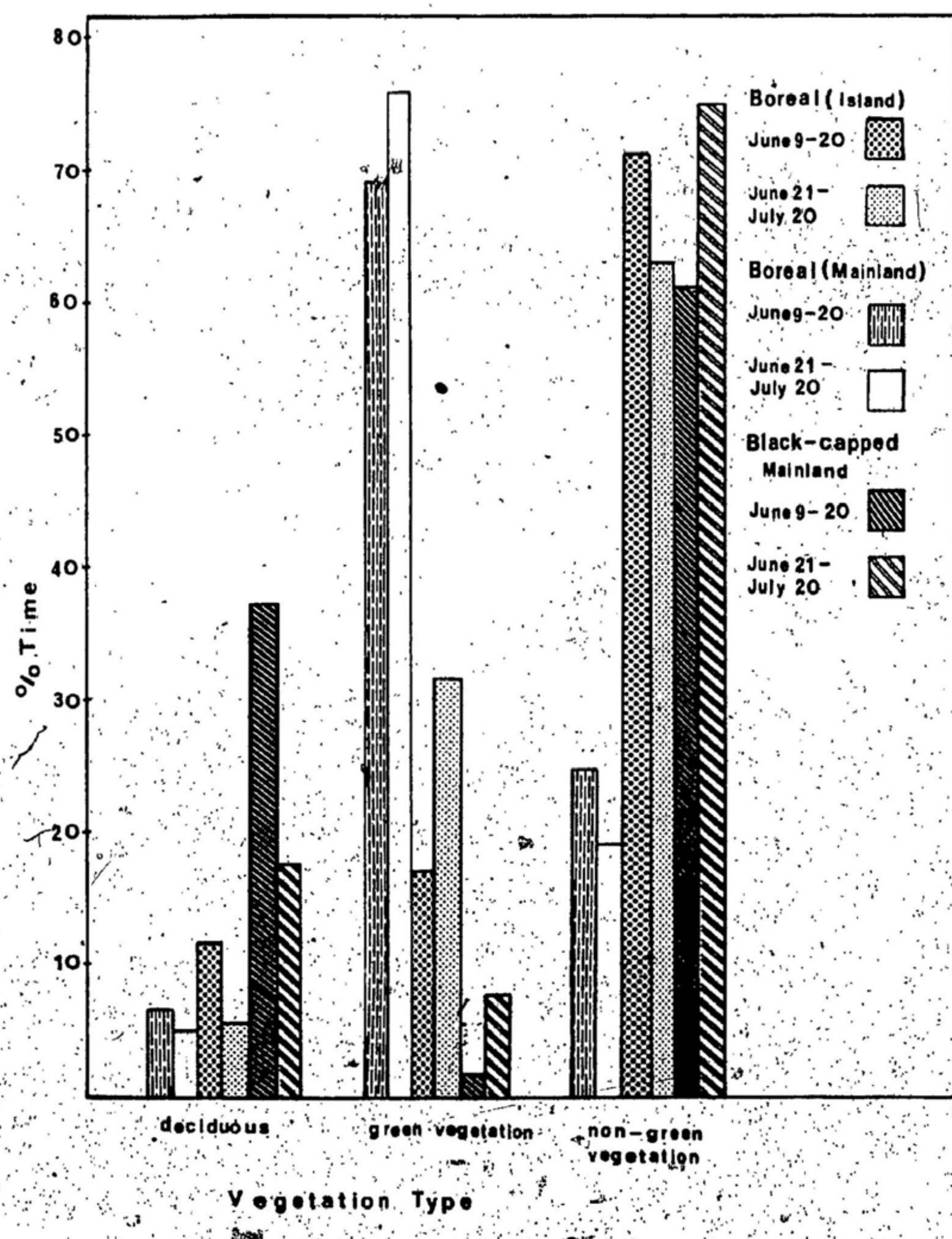
a) Foraging height

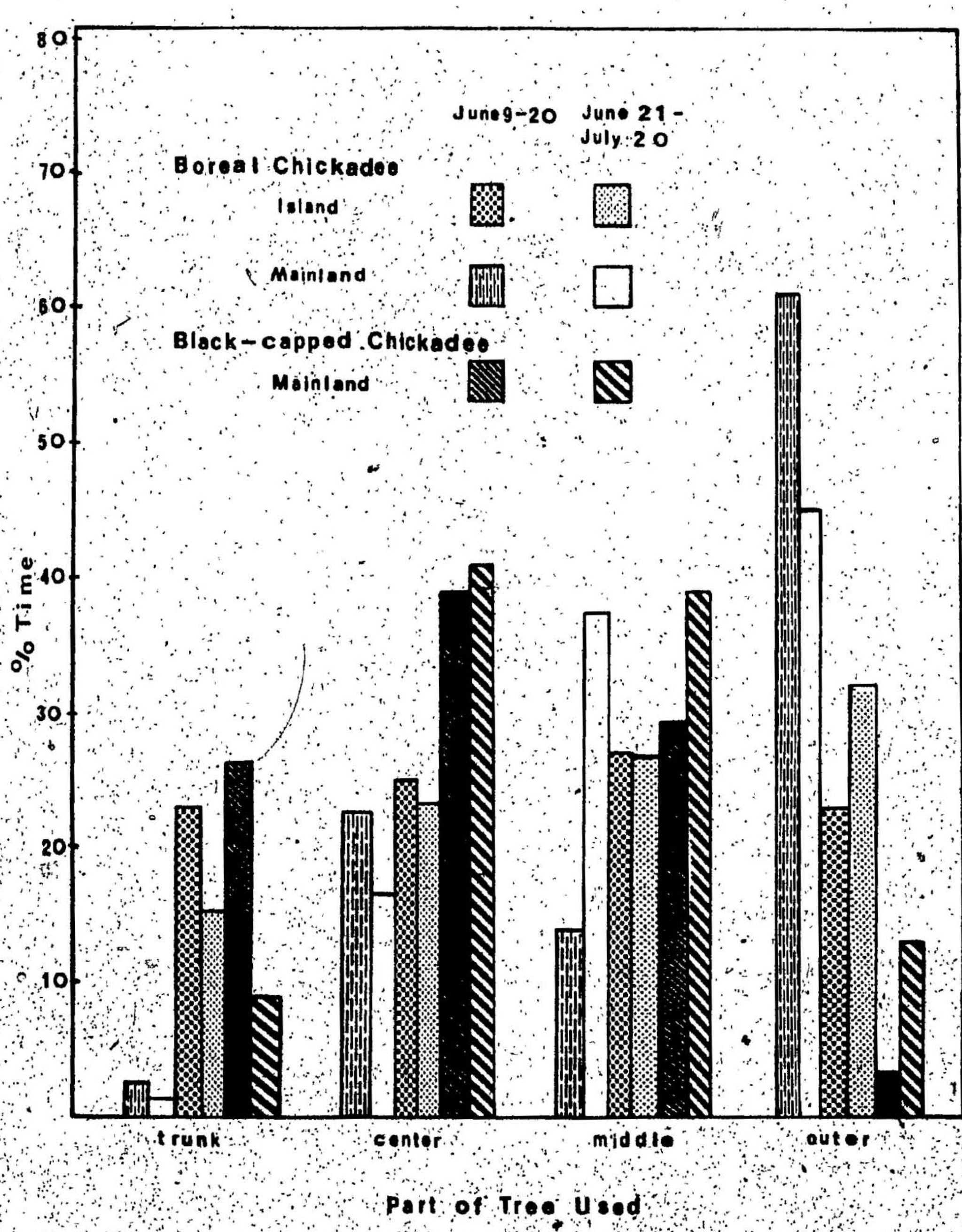
b) Vegetation type

c) Part of tree used



June 9-20
June 21-
July 20
Boreal Chickadee
Island
Mainland
Black-capped Chickadee
Mainland
% Time
80
70
60
50
40
30
20
10
ground
ground→0.30
0.30≤1.52
1.52≤3.05
3.05≤6.10
>6.10
Foraging Height


80
70
60
50
40
30
20
10
% Time
Boreal (Island)
June 9-20
June 21-July 20
Boreal (Mainland)
June 9-20
June 21-July 20
Black-capped Mainland
June 9-20
June 21-July 20
deciduous
green vegetation
non-green vegetation
Vegetation Type



80
70
60
50
40
30
20
10
% Time
June 9-20
June 21-
July 20
Boreal Chickadee
Island
Mainland
Black-capped Chickadee
Mainland
trunk
center
middle
outer
Part of Tree Used

Chickadee on the mainland. The mainland Boreal Chickadee decreased both the amount of foraging on the trunk and outer branches but increased its foraging frequency on the middle part of branches. These seasonal differences within species did not eliminate species differences (Table 20). The differences seen in Figure 10 were still observable in each period of the summer. It is likely that the seasonal differences in foraging behavior were related to changes in distribution of prey items (Partridge 1976; Krebs *et al.* 1972) but data on precise distribution of potential prey were not available.

In summary the terrestrial bird community of Gull Island varied in a number of aspects from the adjacent mainland, South Head, Witless Bay. Only half the number of bird species observed on the mainland were seen on Gull Island. These were all of separate genera whereas on the mainland three groups of congeners were noted.

The total bird density of Gull Island was lower than that of the mainland. Individual species, however, did not all have lower densities realtive to the mainland. Some species did not differ; others had higher island densities whereas the rest were less abundant on Gull Island.

Habitat selection by some species differed, to varying degrees, from island to mainland. The Fox Sparrow showed the greatest amount of difference in habitat selection between the island and mainland.

Although no difference was observed in the foraging habitat of the mainland Boreal and Black-capped Chickadees they differed in their foraging behavior.The foraging of the Boreal Chickadee also differedfrom island to mainland. Seasonal differences were observed within the three populations.

Table 20. Seasonal variations in foraging behavior between chickadee populations on South Head, Witless Bay and Gull Island, 1977, using G-test. (Numbers represent G-values).

	Boreal Chickadee (South Head vs. Gull Island)		Boreal vs. Black-capped Chickadees (South Head)	
	June 9-20	June 21-July 20	June 9-20	June 9-July 20
Foraging Height (df = 5)	310.13*	2159.28*	297.69*	877.10*
Vegetation Type (df = 2)	687.71*	837.85*	525.18*	5989.87*
Part of tree Used (df = 3)	396.55*	37.52*	260.82*	757.31*

* $p < 0.005$

DISCUSSION

Relative to the adjacent mainland, Gull Island has an impoverished fauna. Only 13 passerine species were observed on this island during the summer of 1977 whereas 25 species were recorded on a comparable area of mainland (Table 1). Comparable situations have been found on many other islands (e.g. Preston 1962; Crowell 1963; Diamond 1969; Lack 1969; Keast 1970). Furthermore from year to year changes in species composition of island avifauna are commonly encountered. For example Morse (1977) found a yearly turnover rate of 16.7% on some small Maine islands, and Diamond found a turnover of from 17 to 62% on individual islands of the Channel Islands of California from 1917 to 1968.

Lack (1969), Diamond (1969) and Grant (1966c) all found that the number of species on islands remained fairly constant whereas species changed. Diamond suggested that this could be due to a large chance element in the colonization of islands and the existance of small isolated populations.

Haycock (1973) also studied the avifauna of Gull Island, although her work dealt mostly with breeding seabirds. She reportd a greater number of species than were observed in this study, 15 during the summers of 1967 and 1968, and 34 between 1969 and 1971. However, during that period 19 of the 34 species were absent at least one year from the island (Threlfall, pers. comm.). Thus the expected turnover of species is occurring on Gull Island. That Haycock (1973) reported more species also reflects her census conducted during migration (10 species not found in this study were only seen by Haycock in May and June) and that she censured all habitats, not just those comparable to habitats found in the mainland transect.

Gull Island had a depauperate fauna relative to the mainland. Two species, however, were found only on the island, the Winter Wren and the Brown Creeper. According to Cody (1974) wrens appear to be remarkable colonists. Virtually all North Temperate species have reached offshore islands. The preferred habitat of the Winter Wren is damp areas with luxuriant growth of ferns and mosses (Bent 1964b; Godfrey 1066). The Brown Creeper was only encountered twice. It is found primarily in mature woodland (Godfrey 1966). The forest of Gull Island is mature and shows the effects of windfall. The mainland has second growth forest which has not yet reached maturity. Thus for both these species absence of suitable habitat on the mainland appears to be an adequate explanation for their absence on South Head.

The Raven was not a frequent species on South Head where it was only seen in August, after the young had fledged. One pair nested on Gull Island. Haycock (1973) reports similar events in the past. Ravens frequently nest on islands, on both Pacific and Atlantic coasts, especially where seabird colonies are present (Bent 1964a). They also tend to nest on cliffs (Tuck 1967) as was observed on Gull Island in 1977.

A number of factors were probably responsible for the lower species diversity on Gull Island. A number of authors contend that habitat diversity decreases with a reduction in island size (Anderson 1960; Crowell 1962, 1963; Diamond 1965; Lack 1966; MacArthur and Wilson 1967; Power 1976). Relative to the mainland transect, the island appeared to have a lower habitat diversity. Some of the habitats present on Gull Island were uncommon and not part of the transect. Colonies of seabirds nesting on the slopes and grassy areas (Gulls and Puffins) could have been excluding passerines from this habitat, helping to further reduce the range of available habitat. No such colonies were present on South Head.

A number of species not seen on Gull Island were probably absent due to lack of habitat. Crows and Starlings prefer cut over and agricultural land; Rusty Blackbirds are often associated with bogs, Swamp Sparrows with marshes and Savannah Sparrows with barrens (Tuck 1967). These habitats were either uncommon or not present on Gull Island, whereas most could be found on South Head.

Approximately half of the mainland species absent from Gull Island may be found in ecotonal habitat (Godfrey 1966; Tuck 1967). Although such habitat was present on Gull Island it was not as frequent as on the mainland. This type of habitat may be too small to support self-perpetuating populations of certain species (Anderson 1960; Crowell 1963), therefore excluding them from Gull Island. The presence of large colonies of seabirds may also have rendered some ecotonal areas, between forest and grassy areas, unavailable for passerines.

Decreased habitat diversity may lead to increased competition which in turn may exclude a number of species from Gull Island. This is often noted in the scarcity of congeners present on islands (Grant 1965a, 1966a, 1968). In this study no congeners were noted on Gull Island whereas three groups were observed on the mainland: two *Corvus*, two *Parus* and two *Loxia*. One of each pair was reported on Gull Island.

Haycock (1973) reported five groups of congeners on Gull Island between 1969 and 1971. These congeners were present together for at least one year during this period. In one pair, however, one species was only reported once. Of the remaining four groups only one had both species present on South Head in 1977.

The member of the congener pair found on Gull Island in this study was consistently the species with the most northerly distribution (Godfrey 1966; Robbins and Zim 1966). In the case of Haycock's (1973) findings the most abundant was also the most northerly one except for the Golden-crowned Kinglet which was the more abundant in 1969 relative to the Ruby-crowned Kinglet.

The effect of isolation on species dispersal to Gull Island was probably minimal. The island lies only 1.6 km from the mainland, therefore problems of dispersal should be very low. Morse (1971) found evidence that birds breeding on Maine islands, more than 7 km from the mainland, shared a common gene pool with the mainland. The islands were therefore readily accessible. Morse's findings suggest that South Head species have easy access to Gull Island. Approximately half of the island species are migrants which would be dispersing every spring. Whether or not populations of various species on Gull Island belong to the same gene pool as the mainland populations is a question for further study although the answer might vary with species.

Severity of climate has been suggested as a factor leading to the paucity of insular faunas (Anderson 1960; MacArthur and Wilson 1963). The vegetation of Gull Island does not suggest a climate more severe than on the mainland. The area supported a luxuriant growth of ferns and mosses in the forest understory. This is probably the result of frequent fog leading to a very moist environment. Heavy winds may actually help blow to the island some species that would not otherwise be present.

Since isolation and climatic conditions do not appear to play an important role in the impoverishment of Gull Island's terrestrial avifauna, increased habitat diversity due to the island's small size are probably responsible for the observed low species numbers.

The characteristic impoverished fauna of islands was clearly seen on Gull Island, even relative to Newfoundland, an already species-poor island relative to mainland Canada. The lower number of species present in more northern latitudes did not appear to have a dampening effect on this "island effect".

The total density of passerine birds on Gull Island was lower than on the adjacent mainland, South Head (Table 3). Diamond (1970b) also observed lower densities on satellite islands of New Guinea. Most island bird densities, however, tend to be higher than on comparable mainlands (Anderson 1960; Crowell 1962; Grant 1965a, 1966b; MacArthur, Diamond and Karr 1972; Diamond 1973). Islands with high bird densities usually have two or three species whose densities are much greater than the rest (Cody 1971; Grant 1965a, 1966b; Crowell 1961,1962). These two or three species can make up as much as 80% of the total bird density (Crowell 1962). On Gull Island it took five species to make up over 80% of the total individuals.

On species poor islands such as Gull Island, competition should be greatly reduced. Here only half as many species were present compared to the mainland. The higher densities of three species (Northern Waterthrush, Boreal Chickadee and Gray-cheeked Thrush) on Gull Island are probably the result of such reduced competition. Although the absence of a number of species is probably responsible for the higher densities of

Northern Waterthrush and Gray-cheeked Thrush, the greater abundance of the Boreal Chickadee can be taken to be due largely to the absence of only one species, the Black-capped Chickadee. The total population of Boreal Chickadee on Gull Island was equal to that of both species on the mainland (Table 6). During the month of June the island densities were even higher than those on the mainland. It is possible that the island is providing more suitable habitat than the mainland. This, and the quantified broadening of the niche of the Boreal Chickadee permits higher densities. Diamond (1973) and Lack (1976) have suggested that such a broadening accompanies density changes in depauperate faunas.

The Pine Siskin and the Fox Sparrow had similar densities on both the mainland and island. This may simply be due to these species occupying a similar habitat. Lack of competition might also enable them to occupy a greater portion of a habitat that is suboptimal. All other species found at both areas had lower densities on Gull Island or their numbers at both areas were too low to compare. Diamond (1970b) has also suggested that lower densities could be the result of species broadening their niche into suboptimal habitat.

Differences in niche use between Gull Island and the adjacent mainland were also studied. Investigation of habitat utilization was restricted to three species common enough in both areas to permit comparisons. These were the Northern Waterthrush, Fox Sparrow and Boreal Chickadee. In all cases some differences were observed in habitat use between the mainland and island.

The Boreal Chickadee showed the least difference in habitat use between the island and mainland whereas the Fox Sparrow showed the most variation

(Table 16). All three species showed flexibility of niche by exploiting available habitat which differed in absolute properties between island and mainland. The differences in habitat were probably a reflection of the second growth forest on the mainland and the mature forest on the island.

Broadening of the niche was also observed in all three species. The Boreal Chickadee exploited a greater range of tree densities on the island whereas the Fox Sparrow was found within a greater range of tree heights. On the island the Northern Waterthrush expanded to areas which lacked water. Every Northern Waterthrush habitat investigated on the mainland was associated with either a stream or a small bog as is usual for the species (Godfrey 1966).

A shift in preference was only noted in the Fox Sparrow habitat where the island population shifted towards high numbers of White Birch shrubs. Although the changes in habitat observed in the three species reflect differences in the predominant habitat they were nevertheless changes which show flexibility of the ecological attributes of the species.

The shifts and the broadening of habitat were not accompanied by changes in the density of the Fox Sparrow. The density of the Northern Waterthrush and Boreal Chickadee increased. Most of the increase in the Waterthrush density was probably the result of the species invading areas which lacked water, therefore increasing the amount of potential habitat.

The second investigation of niche shift was of foraging behavior. It involved the two congeners of the genus *Parus*, Boreal and Black-capped Chickadees. They were common and occurred together in the same habitat on the mainland (Table 16). Other studies have found that congeneric species in similar habitats commonly segregate foraging space by vertical layer (MacArthur 1958;Davis 1957;Cody 1968,1974; James 1976;lack 1976) or site (Lack 1971), although not by food items (Cody 1968; Hespenheide 1975). Such trends have also been observed between the sexes of one species (Ligon 1968; Morse 1971; Williamson 1971).

Members of the genus *Parus* have consistently been found to partition foraging space by position and behavior (Hartley 1953; Gibb 1954;Dixon 1961; Root 1964; Smith 1967; Sturman 1968; Lack 1971; Alerstam and Ulfstrand 1977; Morse 1978). Dixon (1961) found that Boreal Chickadees foraged at greater heights than Black-capped Chickadees and preferred coniferous forest to deciduous forest.

In this study Boreal and Black-capped Chickadees exploited different areas of the same habitat (Tables 17a,b,c). The Boreal Chickadee was found higher in trees, sometimes foraging at heights exceeding 6.1 meters. The Black-capped Chickadee foraged closer to the ground and never above 6.1 meters. The Boreal Chickadee was found mainly on evergreen trees, exploiting the live green needles of the middle and outer tips of branches, including the crown of trees. The Black-capped Chickadee spent the majority of its time on evergreen trees but it foraged in areas lacking needles, i.e. bare branches and trunks, near the center of the tree, close to the trunk. It spent more time on deciduous trees than on the live part of evergreens, the area preferred by Boreal Chickadees. Although overlap did occur in these areas, segregation appears to have been extensive enough to permit coexistence.

On Gull Island only one chickadee species was present. The island Boreal Chickadees not only increased in density, becoming comparable to the combined density of both mainland species (Table 6) and shifted foraging habitat to some degree (Table 16) but they also shifted in foraging behavior relative to the mainland population (Tables 17 a,b,c). The island Boreal Chickadees tended to forage at greater heights than the mainalnd population. It spent more time on deciduous trees than on the mainland but not as much as did the mainland Black-capped Chickadee. One significant change was the shift in exploitation from green needles on the mainland to bare branches and trunks on the island. This shift was towards the preferred mainland Black-capped Chickadee foraging area. Such a shift could possibly correspond to the available vegetation on Gull Island where dead trees were common and mature trees offered a greater proportion of bare limbs and branches. The preference for outer parts of branches observed on the mainland was not noted on Gull Island. Here the distribution along the branches was much more uniform from tips of branches to trunk, a shift towards preferred Black-capped Chickadee areas. The shift of the island Boreal Chickadee towards some preferred Black-capped areas supports the hypothesis of an ecological response to absence of competition from Black-capped Chickadees on Gull Island.

Changes in foraging behavior have been noted on other islands (Lack and Southern 1949; Crowell 1962; MacArthur, Recher and Cody 1966; Morse 1967, 1971; MacArthur, Diamond and Karr 1972). These changes are shifts that occur quickly in response to reduced competition pressure (Cody 1971). Genetic change need not be involved.

Although the island populations tended to show shifts in ecological parameters reflecting changes in occurrence of the aspects of the habitats, the populations still were actively showing preferences for some attributes of the island over other attributes rather than passively occupying whatever was available. This point is supported by the seasonal shifts observed in the foraging behavior of each chickadee population. Each population foraged higher up in trees, more on green vegetation, less on deciduous trees and less near the trunk, in the second part of the summer (Figure 11a,b,c). Both mainland and island Boreal Chickadees decreased their foraging time on non-green vegetation whereas the Black-capped Chickadee showed an increase in this type of vegetation, possibly in response to the mainland Boreal Chickadee's shift away from this area. The mainland Boreal increased the time spent on the middle part of branches and decreased its foraging frequency around the periphery of trees whereas both the mainland Black-capped and the island Boreal Chickadees were more frequently observed on outer branches than they had been in the early part of the summer.

Seasonal changes in foraging behavior have been noted in English Tits (Gibb 1954; Hartley 1953). The changes are most notable when winter and summer results are compared and include a number of different parameters including the ones investigated in this study. The slight changes in all aspects of foraging behavior noted in this study are probably only a slight indication of greater yearly trends.

In summary the results appear to support the hypothesis that differences in diversity may result in changes in density and niche use. Along with lower diversity compared with the adjacent mainland Gull Island's terrestrial avifauna also showed changes in habitat use and foraging behavior.

SUMMARY

Gull Island had approximately half the number of passerine species found on the adjacent mainland, South Head, Witless Bay. It appeared that yearly changes in species composition were occurring. The reduced number of island species was probably the result of Gull Island's small size and accompanying lower habitat diversity. Although three groups of congeners were observed on the mainland, none were reported on Gull Island. These species relationships vary from year to year.

Total island bird density was lower than for a comparable area of mainland. Densities of individual species varied. The Northern Waterthrush, Boreal Chickadee and Gray-cheeked Thrush were more abundant on Gull Island. This could have been the result of reduced competition. In the case of the Boreal Chickadee it is possible that the absence of the Black-capped Chickadee was solely responsible. The Fox Sparrow and Pine Siskin had similar densities in each area. They were either exploiting habitat with comparable suitability or were both increasing density in optimal habitat and spreading to more suboptimal habitat where they maintained densities lower than those on the mainland. All other species with large enough densities to compare had lower island densities, probably the result of not enough suitable habitat or the exploitation of suboptimal habitat without compensatory increases in density in optimal areas.

Differences in niche were noted between the Gull Island and South Head populations for both habitat and foraging behavior of species examined. The Boreal Chickadee shifted its selection of foraging habitat in a number of parameters towards the predominant habitat types of Gull Island. It also exploited a broader range of tree densities within the island frequency in green vegetation and foraged less on deciduous trees during the latter part of the summer. Whereas both Boreal Chickadee populations decreased the time spent foraging on non-green vegetation, the Black-capped Chickadee was more frequent in these areas. The island Boreal and the mainland Black-capped Chickadees foraged less near the trunk and more towards the outer part of branches whereas the mainland Boreal Chickadee moved from the trunk and outer branches towards the middle. All these changes did not affect between-population differences. They were probably a reflection of greater yearly trends.

The findings of this study are consistent with current island biogeography theory. Gull Island had a lower diversity of terrestrial bird species as well as an absence of congeners. The total density of birds was also lower than on the mainland. Presumably as a response to lowered competition on the island, a few individual species had higher island densities. Furthermore niche shifts were noted in both habitat and foraging behavior for the species examined. These responses were attributed to both changes in the structure and composition of the habitats available and to the lowered levels of interspecific competition on the island.

habitat indicating ecological release. Shifts in the Northern Waterthrush habitat also occurred in the direction of the predominant island habitat. The Waterthrush also expanded into areas that lacked water. This probably accounted for their higher density. The Fox Sparrow showed the greatest change in habitat utilization. This again corresponded to a change in predominant habitat between the mainland and island. Again evidence favored release as well as simple niche plasticity, as a broadening occurred in the range of tree heights found within the habitat.

On South Head the two chickadee species, Boreal and Black-capped Chickadees were found together. They coexisted by exploiting different areas of the vegetation. The Boreal Chickadee foraged higher and mainly on the green needles found in the middle and outer branches. The Black-capped Chickadee was found at lower heights. It spent more time on branches near the trunk which lacked green vegetation. It was also more common on deciduous trees.

Shifts were noted in the foraging behavior of the Boreal Chickadee on Gull Island. It spent more time on deciduous trees but not as much as did the Black-capped Chickadee on South Head. Foraging occurred at greater heights on trees than either mainland populations. Instead of foraging mostly on green needles, as it had on the mainland, the island Boreal Chickadee foraged mostly on dead or bare branches, a shift towards areas used on the mainland by Black-capped Chickadees. It foraged evenly from the tips of branches to the trunk and did not restrict itself to the outer parts of trees.

Changes were noted in foraging behavior within each population during the summer. Each group foraged at greater heights, increased their

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