TABLE 1. Breeding phenologies of thrushes on Langara Island, British Columbia, 1971.

Species	Date first seen in spring	Date fledged young first seen
Hermit Thrush	16 April	20 June[a]
Swainson's Thrush	6 June	11 July
Robin	25 March	—
Varied Thrush	26 March	21 June

[a] Fledged young Hermit Thrushes were first observed in 1970 on 12 June.

son's Thrushes forage along the upper beaches and nest, usually within 500 m of the beach, on stumps and tree trunks in a mixed forest of western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*). Robins and Varied Thrushes also forage along the upper beaches and nest along the periphery of the island but place their nests higher than those of Hermit and Swainson's Thrushes. Ecological segregation among these thrushes there, particularly between Hermit and Swainson's Thrushes, is achieved primarily by their different breeding phenologies (table 1).

The Hermit Thrush returns to Langara Island about 6 weeks earlier than the Swainson's Thrush and the former's young have begun to fledge by about the time the Swainson's Thrush arrives in mid-June. Adult and young Hermit Thrushes forage along the beaches until at least mid-August (when my observations ceased in 1971); adult Swainson's Thrushes and their young, after mid-July, also foraged along these beaches but had dispersed from the island by the end of July. I do not know whether both species took the same prey items. A similar differential timing of breeding also occurs on Forrester Island, Alaska (Willett 1915; Bailey 1927), some 70 km N of Langara Island.

These observations were made during ecological studies of seabirds on and near Langara Island from 6 May to 10 July 1970 and from 17 March to 10 August 1971.

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GENETIC STRUCTURE OF TWO POPULATIONS OF WHITE-CROWNED SPARROWS WITH DIFFERENT SONG DIALECTS

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INTRODUCTION

Intraspecific geographic variation in passerine bird song over ranges of a few miles or less has been described in several species (Marler and Tamura 1962; Lemon 1966; Nottebohm 1969). The occurrence of several males singing similar songs in the same local area has produced the concept of dialect populations. In some cases it has been shown experimentally that such a dialect is learned during the early ontogeny of the individual (Thorpe 1958; Marler and Tamura 1964; Dittus and Lemon 1969; Marler 1970).

Over a decade ago Marler and Tamura (1962) argued that "The stereotypy and stability of the song 'dialects' suggest that little exchange of individuals between populations occurs after the song patterns have been learned. Thus in this case there may be a potential relationship between song 'dialects' and the genetic constitution of populations, either indirect, if young birds simply do not wander far, or direct, if they wander but are attracted to breed in areas where they hear the song type which they learned in their youth."

The effects of this pattern of occurrence and acquisition of song on social behavior and genetic structure of the species have just begun to be explored (Verner and Milligan 1971; Nottebohm and Selander 1972).

The most general evolutionary question we wish to be able to answer is what is the function of song dialects? This question is improper without some qualification since dialects are culturally acquired. It is the ability to acquire a song by copying a model heard during early life that can be selected for and not the dialect. Thus, it is the method of song attainment that may be an adaptation. The research hypothesis being examined in this and subsequent reports is that song dialects in White-crowned Sparrows (*Zonotrichia leucophrys*) act as behavioral barriers to gene flow. We also ask what are the genetic consequences of such an island population structure.

Data on dispersal, mate selection, and possible selection differentials between populations are currently being accumulated. A preliminary examination of the genetic constitution of two dialect populations has been completed and is the subject of this report. The results cannot discriminate between the island model and isolation by distance.

MATERIALS AND METHODS

Subjects. In the fall of 1971, White-crowned Sparrows (*Zonotrichia leucophrys nuttali*) were captured live from two locations in the coastal chaparral belt

TABLE 1. Electrophoresis conditions for examination of proteins coding for presumptive loci.

Protein assayed	Tissue used	Buffer conditions
Aspartate aminotransferase	M	LH
Acid phosphatase	L	LH
Adenosine deaminase	M	LH
Catalase	L	TC
Creatine kinase	M	LH
Glucose phosphate isomerase	L	TB
Hemoglobin	H	TB
Isocitrate dehydrogenase	L	TC
Leucine amino peptidase	L	TC
Lactate dehydrogenase	M	LH
L-leucylglycylglycine peptidase	L	TC
L-leucyl proline peptidase	L	TC
Mannose-6-phosphate isomerase	M	LH
Malate enzyme	L	TC
Malate dehydrogenase	L	TC
Nucleoside phosphorylase	L	LH
Peroxidase	L	TC
6-phosphogluconate dehydrogenase	L	TB
Phosphoglucomutase	L	TC
Serum proteins	S	LH
Xanthine dehydrogenase	L	TC

M = muscle, L = liver, S = serum, H = hemoglobin; LH = lithium hydroxide pH 8.3 discontinuous buffer; TB = tris EDTA borate pH 8.6 continuous buffer; TC = tris citrate pH 6.2 continuous buffer.

of central California. One sample of 38 individuals was taken from a single site in Marin County and a second of 39, from a location in San Mateo County about 40 air miles south. The birds were shipped live to New York where subsamples of 10 San Mateo males and 8 Marin males were induced to sing by implants of testosterone under the skin of the neck.

Song analysis. Songs were recorded indoors with a Tandberg taperecorder and either a Sony or Tandberg microphone. Sonograms were prepared on a Kay Electric spectrum analyzer. Usually at least 10–20 songs were examined from each bird to evaluate individual variation.

Electrophoretic analysis. Following song induction, the pellets were removed and several weeks later the birds were killed for electrophoretic analyses of tissue proteins. Twenty-two presumptive genetic loci coding for enzymes and nonenzymatic proteins were examined. Liver, muscle, and blood were used in the analyses. Electrophoresis was horizontal on starch slabs, using filter paper squares to take up the extracts produced by squashing the tissues with a glass rod. Most runs were 4–6 hr at 250–300 volts. Staining procedures were adapted from Brewer (1970) and Shaw and Prasad (1970). Buffer conditions and tissues used for each assay are given in table 1.

RESULTS

Song patterns. Sonograms of 10 different songs from the same male are shown in figure 1. This degree of stereotypy was typical. Therefore, the population samples shown in figures 2 and 3 are representative of the variation within each dialect group

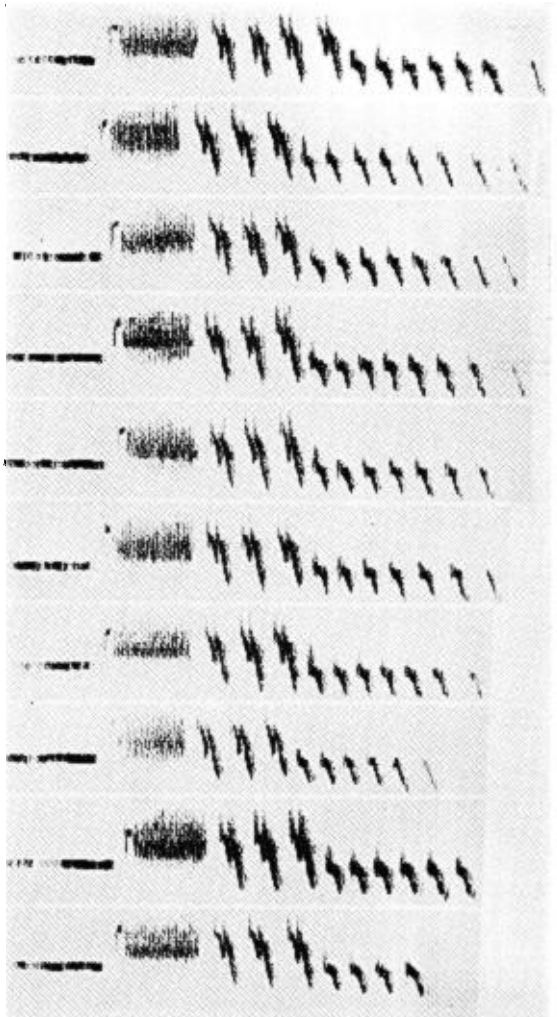

FIGURE 1. Sonograms of 10 songs of one Marin male. Vertical axis is sound frequency. Horizontal axis is time. Songs are approximately 2.3–2.5 sec long.

and the distinctiveness of the two populations. The segment of the song that seems to be consistent within a population and differentiates the two populations is the terminal portion. The Marin males have songs containing note type A followed by type B, whereas San Mateo males lack type B notes and may have type C at the end (figs. 2 and 3). In the summer of 1972, I visited both areas where the birds were collected and found that the songs induced in the captive birds were quite typical of the naturally singing males.

Electrophoretic analyses. Twenty-two presumptive genetic loci were analyzed and read with confidence. Eight other enzyme systems were examined but could not be repeated and interpreted without ambiguity. These were esterase, glucose-6-phosphate dehydrogenase, l-leucyl-tyrosine peptidase, adenylate kinase, alkaline phosphatase, fumarase, sorbitol dehydrogenase, and alcohol dehydrogenase. The 22 presumptive loci used for analysis comprise 12 invariant and 10 variable (45%) loci. Two of these 10 were nearly fixed for the fast allele of a two allele locus, each having one heterozygote in the total sample. The

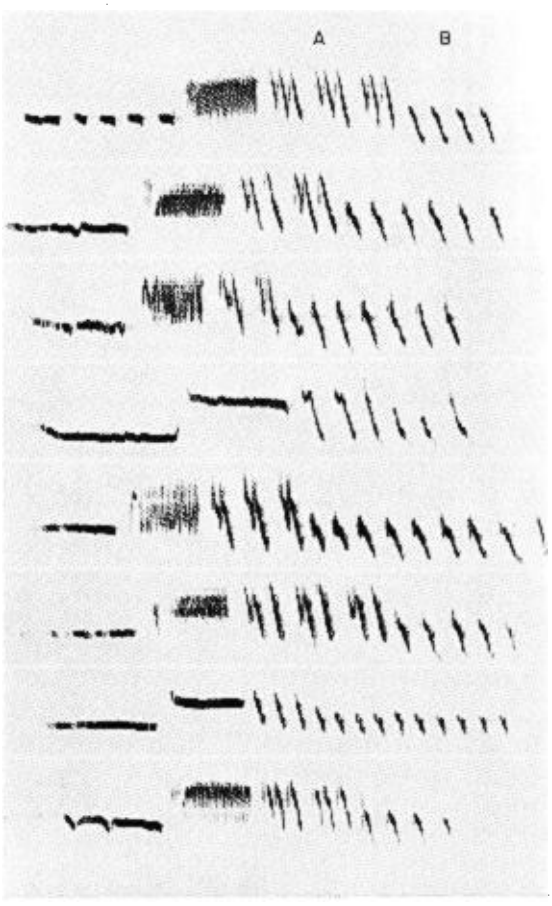

FIGURE 2. Sonograms from each male in the Marin sample. Note types A and B are indicated.

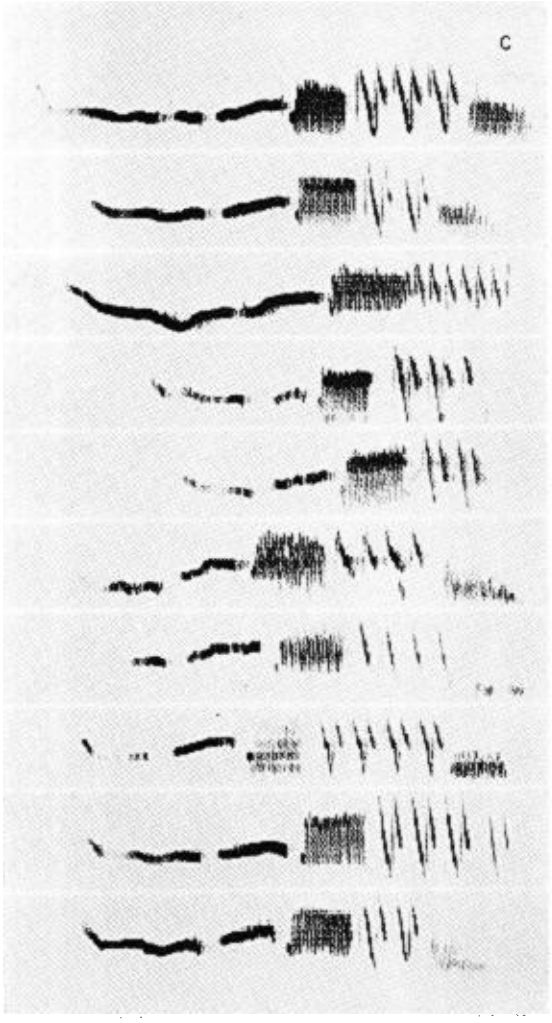

FIGURE 3. Sonograms from each male in the San Mateo sample. Note type C is indicated.

average individual was heterozygous for 9.2% of its loci in the San Mateo population and 8.7%, in the Marin population. Most of the variable loci were segregating for two alleles. Four alleles were found for 6-phosphogluconate dehydrogenase and three for the B-locus of phosphoglucomutase.

Gene frequencies. Four loci (PGM-A, L-PRO, L-GLY-C, 6-PGDH) that exhibited the greatest degree of variation were examined for sexual differences in both populations. These results are shown in table 2. None of the eight groups gave significant differences by Chi square with continuity correction (Siegel 1956). Therefore, males and females were combined for comparing populations. Table 3 gives gene frequencies of the 10 variable loci for each population. All loci were tested for significance of differences between populations and one of the 10 (PGM-A) was found to differ significantly.

The proportion of loci that are significantly different between populations is probably dependent on sample size. To gain further understanding of the degree of difference between the populations, we can employ an index of overall similarity. The percent overlap at each locus was calculated according to the method of Horn (1966) for ecological overlap and adapted by Hedrick (1971) to genetic data.

TABLE 2. Comparison of gene frequencies of males and females at four presumptive loci.

	Locus	PGM-A		L-PRO		L-GLY-C		6-PGDH			
	Allele	f	s	f	s	f	s	a	b	c	d
San Mateo	Males	0.48	0.52	0.16	0.84	0.18	0.82	0.00	0.52	0.46	0.02
	Females	0.57	0.43	0.40	0.60	0.25	0.75	0.03	0.47	0.43	0.07
Marin	Males	0.73	0.27	0.18	0.82	0.18	0.82	0.06	0.47	0.47	0.00
	Females	0.80	0.20	0.25	0.75	0.14	0.86	0.02	0.50	0.46	0.02

TABLE 3. Gene frequencies for 10 presumptive loci for both populations.

Locus		F	S	C	D
Acid phosphatase	Marin	0.90	0.10		
	San Mateo	0.93	0.07		
Adenosine deaminase	Marin	0.96	0.04		
	San Mateo	0.92	0.08		
Glucose phosphate isomerase	Marin	0.90	0.10		
	San Mateo	0.92	0.08		
Isocitrate dehydrogenase	Marin	1.00	0.00		
	San Mateo	0.99	0.01		
L-leucylglycylglycine peptidase (C)	Marin	0.16	0.84		
	San Mateo	0.22	0.78		
L-leucyl proline peptidase	Marin	0.21	0.79		
	San Mateo	0.23	0.77		
6-phosphogluconate dehydrogenase	Marin	0.04	0.49	0.46	0.01
	San Mateo	0.01	0.50	0.45	0.04
Phosphoglucomutase (A)	Marin	0.77	0.23		
	San Mateo	0.50	0.50		
Phosphoglucomutase (B)	Marin	0.01	0.05	0.94	
	San Mateo	0.01	0.12	0.87	
Serum protein	Marin	0.99	0.01		
	San Mateo	1.00	0.00		

Results given in table 4 indicate that about 96% of the genomes of the two populations overlap (4% nonoverlap). This corresponds closely to the Chi-square results which showed one locus of the 22 examined (4.5%) had significantly different gene frequencies between the two populations.

Table 5 shows the observed genotype frequencies and Hardy-Weinberg expectations for 7 of the 10 variable loci. One of the O-E differences, San Mateo L-PRO, was significant.

Table 6 examines the possibility of genetic differences between age groups. Two age classifications are possible for adult *Z. l. nuttali*. First-year birds do not attain a fully adult crown pattern. Usually, large amounts of brown feathers are present in the black and white areas of the crown, and these individuals are known as "brown crowns" (Ralph and Pearson 1971). Birds in their second breeding season and older develop a fully black- and white-crown pattern. The four most variable loci were used for this comparison. No significant age differences were found in any of the eight Chi-square tests.

Heterozygosity. The frequency distributions of the number of heterozygous loci for individuals of the two age groups are compared in figure 4. There seems to be a tendency toward a greater degree of heterozygosity in older birds. A test of significance between the two distributions, however, could not show them as different. Thus it cannot be concluded from figure 4 that there is directional selection toward greater heterozygosity as birds age.

TABLE 4. Percent overlap[a] at each locus between the two populations.

Locus	Percent overlap
Adenosine deaminase	99
Acid phosphatase	98
Glucose phosphate isomerase	98
Isocitrate dehydrogenase	99
L-leucylglycylglycine peptidase	98
L-leucyl proline peptidase	93
Phosphoglucomutase—A	82
Phosphoglucomutase—B	96
6-phosphogluconate dehydrogenase	99
Serum proteins	99
Mean Overlap	96

[a] Percent overlap $= \dfrac{\sum_{j=1}^{n} P_{j\cdot x} P_{j\cdot y}}{\frac{1}{2}\left[\sum_{j=1}^{n} P_{j\cdot x}^{2} + \sum_{j=1}^{n} P_{j\cdot y}^{2}\right]} \times 100$

$P_{j\cdot x}$ = frequency of j^{th} genotype in population X; $P_{j\cdot y}$ = frequency of j^{th} genotype in population Y; n = number of genotypes at a given locus.

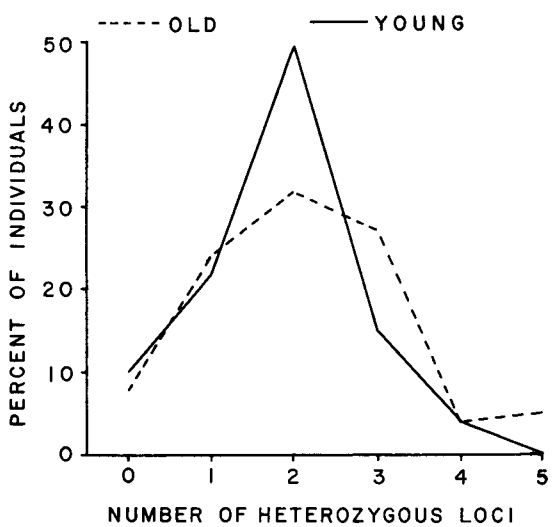

FIGURE 4. Comparison of the number of heterozygous loci in young and old birds.

TABLE 5. Observed genotype frequencies and Hardy-Weinberg expectations for seven variable loci.

Locus	Population	p^2		$2pq$		q^2		$2pr$		$2rq$		r^2	
		E	O	E	O	E	O	E	O	E	O	E	O
Phosphoglucomutase (B locus)	Marin	0	0	0	0	1	1	3	4	1	0	34	34
	San Mateo	0	0	1	1	0	0	8	6	0	1	29	30
Glucose phosphate isomerase	Marin	31	31	7	8	1	0						
	San Mateo	32	32	6	6	0	0						
L-leucylglycylglycine peptidase (C locus)	Marin	1	0	8	10	22	21						
	San Mateo	2	3	10	7	18	20						
L-leucyl proline peptidase	Marin	1	3	10	7	20	21						
	San Mateo	1	7	11	0	18	23						
Phosphoglucomutase (A locus)	Marin	23	22	14	16	2	1						
	San Mateo	10	10	19	18	9	10						
Adenosine deaminase	Marin	36	36	3	3	0	0						
	San Mateo	32	32	5	6	1	0						
Acid phosphatase	Marin	32	31	7	8	0	0						
	San Mateo	33	33	5	5	0	0						

DISCUSSION

The description of genetic differences between populations is one step in evaluating the significance of song dialects for the genetic organization of populations of White-crowned Sparrows. Actually, no hypothesis is eliminated by this step since gene flow cannot be evaluated from knowledge of gene frequencies in two populations. Genetic similarity of two populations may be caused by similar selective pressures and a small degree of gene exchange. Genetic differences may be the result of differential selection in the face of substantial gene flow.

In the present case, the discovery of considerable electrophoretic variation in White-crowned Sparrows and the apparent differences in allelic frequencies between dialects are important to the solution of the song dialect question. If the allelic frequency differences in the two populations are maintained by differential selection, it opens the possibility for experimentation on the selection pressures involved.

Unfortunately, the significance of dialects for the electrophoretic data presented here is compromised by the substantial distance between samples. It is a real possibility that any genetic isolation may be by distance rather than by communicatory behavior. The existence of behavioral barriers to gene migration must be sought in continuous populations where an insular pattern of behavioral isolates could correspond to genetic isolates. A more complete examination of relationships between song dialects and genetic differentiation is currently under study in an area where two song types come together.

SUMMARY

The potential role of song dialects for population structuring in White-crowned Sparrows was investigated through song recording and electrophoretic analysis of allozymes.

A population from Marin County, California, and one from San Mateo County were found to have differing song types. Twenty-two presumptive genetic loci were examined by biochemical techniques. Ten of the loci were variable. One locus, phosphoglucomutase-A, was significantly different between the two samples by Chi square. An index of overall similarity suggests that the probability of genotypic identity between the two populations is 96%. No significant age or sexual differences were found in gene frequencies.

The average individual in the San Mateo sample was heterozygous for 9.2% of its loci and in the Marin sample for 8.7% of its loci. There appears to be a tendency toward greater heterozygosity in older birds, but this was not statistically significant.

Biochemical techniques applied in this study were learned from T. A. Uzzell, M. Johnson, and R. Storez while I was a graduate student at Yale University. Sound recording and analysis was learned from C. Hopkins, P. Mundinger, and S. Green. Birds were provided through the efforts of W. Mewaldt, J. Sobieski, and L. R. Mewaldt. M. Johnson furnished a critical reading of the manuscript. Financial aid was given by the laboratory of Professor P. Marler, the Rockefeller University. The research was com-

TABLE 6. Comparison of gene frequencies of young and old birds at four loci.

Population	Age	6-phosphogluconate dehydrogenase				Phosphoglucomutase (A locus)		L-leucylglycylglycine peptidase (C)		L-leucyl proline pep.	
		F	S	C	D	F	S	F	S	F	S
San Mateo	Young	0.03	0.47	0.44	0.06	0.60	0.40	0.18	0.82	0.14	0.86
	Old	0.00	0.50	0.50	0.00	0.42	0.58	0.21	0.79	0.32	0.68
Marin	Young	0.06	0.53	0.38	0.03	0.75	0.25	0.04	0.96	0.25	0.75
	Old	0.02	0.48	0.50	0.00	0.79	0.21	0.27	0.73	0.19	0.81

pleted during the tenure of an NSF Postdoctoral Fellowship.

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FOODS AT A GOLDEN EAGLE NEST IN CENTRAL ALASKA

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There is apparently a single published account of foods used by North American Golden Eagles (*Aquila chrysaetos*) north of 60°N Latitude, that of Murie (1944). With the present interest in northern development and with the subsequent need for information relating to all aspects of northern ecology, it seems useful to provide some additional records.

THE STUDY AREA AND NEST SITE

Observations were made at a nest near mile 99 on the Steese Highway (65°24′ N, 145°35′ W) in central Alaska. The nest was 6 miles by road from the ptarmigan research study area of Weeden (1965), and his description of the terrain and vegetation pertains to this study as well. In general, timberline is low, at about 865 m, and much of the area is alpine tundra. The nest site was a north-northwest-facing cliff ledge near the summit (about 1000 m) of one of the low, rounded hills typical of the area. The nest itself had reportedly been used several years in succession and at the time of my first visit, 21 July 1963, was nearly 2 m high. It appeared to consist of alternating strata of sticks and ptarmigan (*Lagopus* sp.) feathers. Two large eaglets, near fledging, occupied the nest ledge at that time. The adults were not seen.

MATERIALS AND METHODS

Prey items in and near the nest were noted on the first visit, and three regurgitated pellets were examined macroscopically. On 30 August, after the eagles had left, I made a more intensive search of the nest area, again noting prey remains. At this time I collected an additional 50 pellets; these were later crumbled and analyzed dry. Prey identifications were made by comparisons with known specimens, including pellets of known composition obtained from a captive eagle. Slides of mammal hairs from the University of Alaska Museum helped in some cases. Data were recorded as frequency of occurrence and estimated percentage volume.

RESULTS AND DISCUSSION

Prey remains. On the July visit, two freshly killed, unplucked, juvenile Willow Ptarmigan (*L. lagopus*) lay at the eaglets' feet and feathers from previous kills were evident over the nest ledge. Ptarmigan remains, mostly plucked feathers, also predominated at the nest and feeding promontory sites at the end of August. At that time I also found some snowshoe hare (*Lepus americanus*) remains and the skull and bits of hide of a marten (*Martes americana*).

Pellet analyses. Table 1 lists the incidence and relative importance of foods identified in the pellets. Ptarmigan constituted the most used item, but it was not possible to determine which of the two species in the area was the more important. Rock Ptarmigan (*L. mutus*), which occur mostly in exposed habitats above timberline, would appear to be more vulnerable, but the high incidence of snowshoe hare in the food pellets suggests that the eagles did effectively hunt Willow Ptarmigan habitats (brushy, lowland areas). Where species identification was possible, four were *L. lagopus* and three were *L. mutus*. There were at least 130 pairs of Rock Ptarmigan present on the 15-square-mile study area just a few miles north of the nest during the year of this study (Weeden 1965). McGahan (1968) cited several reports of bird-dominated eagle diets in Europe, particularly in the heather uplands of the British Isles where, again,