

FORAGING SITES OF ALPINE BIRDS
IN RELATION TO SNOW ACCUMULATION

by

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This is to certify that the thesis prepared by

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ABSTRACT

Foraging locations and behaviors of an avian ground-foraging guild were investigated on Chowder Ridge in the Mt. Baker-Snoqualmie National Forest, Washington, during the summer of 1984. Three species, Water Pipits, Horned Larks, and Rosy Finches, made up the guild. Relative abundances of arthropods as prey items were measured for snow covered and snowfree surfaces.

Birds selected snowfree habitats more often than snow covered areas as foraging sites. Pipits and larks foraged more rapidly and steadily over snow surfaces compared to snowfree areas. However, pipits had higher rates of pecking during foraging bouts on snow cover than larks. Finches were never observed foraging on snow. Relative abundances and diversities of arthropods were considerably greater on snowfree surfaces than on snow cover.

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INTRODUCTION

Alpine environments are open areas of the upper slopes and peaks of mountains. Plants grow low to the ground and are typically angiosperms consisting of perennial herbs or prostrate shrubs (Billings 1974). Alpines are "those physical conditions occurring, on mountains, above the regional climatic upper limits of tree species" (Billings 1974). Low temperatures (even in summer), wind, high intensity solar radiation, a short growing season, and prolonged snow cover typify the alpine. In response to these harsh conditions, a unique fauna and flora have evolved. Although superficially barren, alpine regions contain a flora far richer than that of the similar arctic tundra (Billings 1974).

Persistent snow cover along with extensive snowfree areas provide contrasting breeding and foraging sites for an alpine bird community during the summer. The pattern of snow cover and snowfree areas in the alpine is dynamic, characterized by the exposure of additional food sources at progressively higher altitudes due to the advancing summer season and resultant snowmelt.

Snow generally recedes in the summer in an upslope pattern (Slaymaker 1974). However, other areas exposed to high winds may be snowfree even during the winter. Snow may linger on north slopes throughout the summer, while south slopes may be mostly snowfree by early summer.

Passerine birds exploiting these areas are members of an alpine ground-foraging guild. A guild is defined as a group of species that exploit the same kinds of resources in a similar manner (Root 1967). This guild includes the Rosy Finch (Leucosticte arctoa), Water Pipit (Anthus spinoletta), and Horned Lark (Eremophila alpestris). In addition, the following species have been reported on alpine slopes during the summer and may qualify for guild membership: White-crowned Sparrow (Zonotrichia leucophrys), Dark-eyed Junco (Junco hyemalis), Lincoln's Sparrow (Melospiza lincolni), Chipping Sparrow (Spizella passerina), Vesper Sparrow (Pooecetes gramineus), Cassin's Finch (Carpodacus cassinii), and American Robin (Turdus migratorius) (Hoffman 1960, Weeden 1960, Johnson 1966, Pattie and Verbeek 1966, Norvell pers. observ.). Although the alpine ground-foraging guild is potentially larger, this study focuses on the Water Pipit, Horned Lark, and Rosy Finch. These species forage by gleaning vegetation and snowfields for arthropods during the alpine summer.

Foraging techniques of this guild correspond to Schoener's (1969) description of a Type II predator: an animal which spends energy and time searching for, rather than pursuing, prey. This classification is accurate although the diets of individual guild members are variable. Pipits are almost entirely insectivorous (Martin et al. 1951, Verbeek 1967), while the summer diet of alpine larks consists of 50% to 80% arthropods (Verbeek 1967, 1970; Conry 1978).

Rosy Finches forage for arthropods during the early summer, but consume mostly seeds as the summer progresses (Twining 1940, French 1959, Johnson 1965, Hoffmann 1974).

Arthropods are abundant in alpine meadows where guild members forage. Additionally, potential food items are swept upslope and deposited on the snow by rising westerly air currents and updrafts. In addition, snow may attract airborne insects by acting as a reflective light trap (Edwards 1972). Frequently, the snowbanks and expansive snowfields of the high mountains are littered with bodies of numbed and dead insects (Mani 1962, 1980; Edwards 1972). Twining (1940) estimated insect densities on snow may be as high as 30 to 36 m².

If snowfields are attractive to insects, they may concentrate potential food items. As a result, extensive alpine snowfields may enhance foraging activities of this guild. Snow also influences the nesting and foraging locations of guild members. For example, breeding territories are usually located near snowbanks, and early summer foraging is frequently done on or at the edges of snow (Shaw 1936, Twining 1940, French 1959, Johnson 1965, Pattie and Verbeek 1966, Verbeek 1970, Conry 1978). Larks and pipits often forage on snow surfaces, while Rosy Finches prefer snowbank edges. Pipits select nesting sites at snow accumulation areas because the snowbank offers a greater supply of insects during the early breeding season (Conry 1978).

Optimal foraging theory predicts that birds forage in

areas where the rate of food capture is highest (Goss-Custard 1981). The theory also allows predictions of foraging patterns based on net energy gains per unit of time (Morse 1980). Therefore, birds should spend their time feeding in the most profitable places in the most efficient way. Differences in foraging behavior between snow and snowfree surfaces may indicate which habitats are offering optimal conditions for enhancing economy of effort for these ground-foraging passerines.

Several features of the optimal foraging theory apply to the foraging patterns of this guild. The "patch" concept suggests that foragers have the ability to recognize patches (areas of concentrated food separated from areas of lower food abundances), and either accept or reject them (Morse 1980). Snowbanks may be considered patch habitats if they offer insectivorous birds (a) greater densities of arthropods relative to snowfree, vegetated meadows, or (b) higher availability of arthropods because of their conspicuousness on snow surfaces.

Birds may concentrate their foraging activities on the most conspicuous prey, even in low quality environments (i.e., patches of low prey density), and still forage in an optimal way (Zach and Falls 1976). Arthropods (particularly large ones) on snow surfaces would seem to be conspicuous to a point. of increasing their selective vulnerability as prey.

Foraging rates vary interspecifically and between sexes of a species depending on the stage of the breeding cycle (Morse 1968). Intraspecific variations in foraging rates are sometimes initiated by productive food sites (Pyke 1978). The

number of pecks that a bird makes varies when it encounters productive patches (Verbeek 1970, Smith 1977, Goss-Custard 1981). While observing foraging alpine pipits and larks, Verbeek (1970) noted that pecking rates for both species were considerably higher on snow covered surfaces than in vegetation. He concluded that these birds forage more efficiently on snow because insects are more easily seen.

Another parameter that requires consideration is the optimal foraging period: i.e., concentration of foraging activities at specific times of the day. Optimal periods may depend on (a) availabilities of prey items, and (b) the costs (or dangers) of capturing prey (Morse 1980). Some insectivorous birds concentrate their feeding efforts during the cooler time of day (Morse 1971). Variations may also occur because of diurnal differences in prey availability (Orians 1966). However, foraging periods might be extended toward less profitable times when food is scarce and/or when energy demands are large (Schoener 1971). In alpine habitats, optimum foraging should be negatively correlated with extreme diel fluctuations in weather conditions.

Most previous studies of alpine passerines have focused on breeding activities rather than foraging patterns. The purpose of this study was to investigate the significance of alpine snow covered surfaces as a factor in determining foraging patterns of birds during the summer season. My principal objectives were:

1. to determine foraging habitat use (i.e., where birds-

foraged), and calculate the proportion of foraging time on snow covered surfaces compared to snowfree surfaces;

2. to observe foraging patterns (i.e., how birds feed on snow surfaces versus snowfree areas);
3. to sample and determine comparative prey abundances;
4. To measure various abiotic factors such as air temperature, wind speed and direction; to describe cloud cover and precipitation; and to look for correlations between these factors and foraging habitat patterns.

STUDY AREA

The field study was conducted on Chowder Ridge in the Mt. Baker-Snoqualmie National Forest, Washington, between 14 July and 11 August 1984. The ridge is approximately 5 km long and lies north-northwest along the northern base of Mt. Baker (elevation = 3286 m). Chowder Ridge has a north-west-southeast orientation, adjoining Mt. Baker at its eastern end via Bastille Ridge and Mazama Glacier. Elevation varies from 2032 m to 2312 m at Hadley Peak, the highest point. Both slopes are steep, and the north-facing slope is covered with extensive snowfields and a glacier. The study was confined to the western quarter of the ridge where accessibility was easier and more snowfree areas were found due to earlier snowmelt.

A maritime climate characterizes the western slopes of the North Cascades of which Chowder Ridge is part. Weather is highly variable with frequent thunderstorms, cold drizzle, sleet, and snow throughout the year. Winds are primarily westerly, carrying more precipitation to the western slopes than to the eastern slopes. Mean annual precipitation at the Mt. Baker subalpine weather station is 280 cm (28 cm accumulate during the summer). Mean summer temperature is 12°C and mean annual temperature is 5°C (Douglas and Bliss 1977).

Alpine plant communities on Chowder Ridge have been described by Taylor and Douglas (1978) and those in the

Mt. Baker region by Douglas and Bliss (1977).

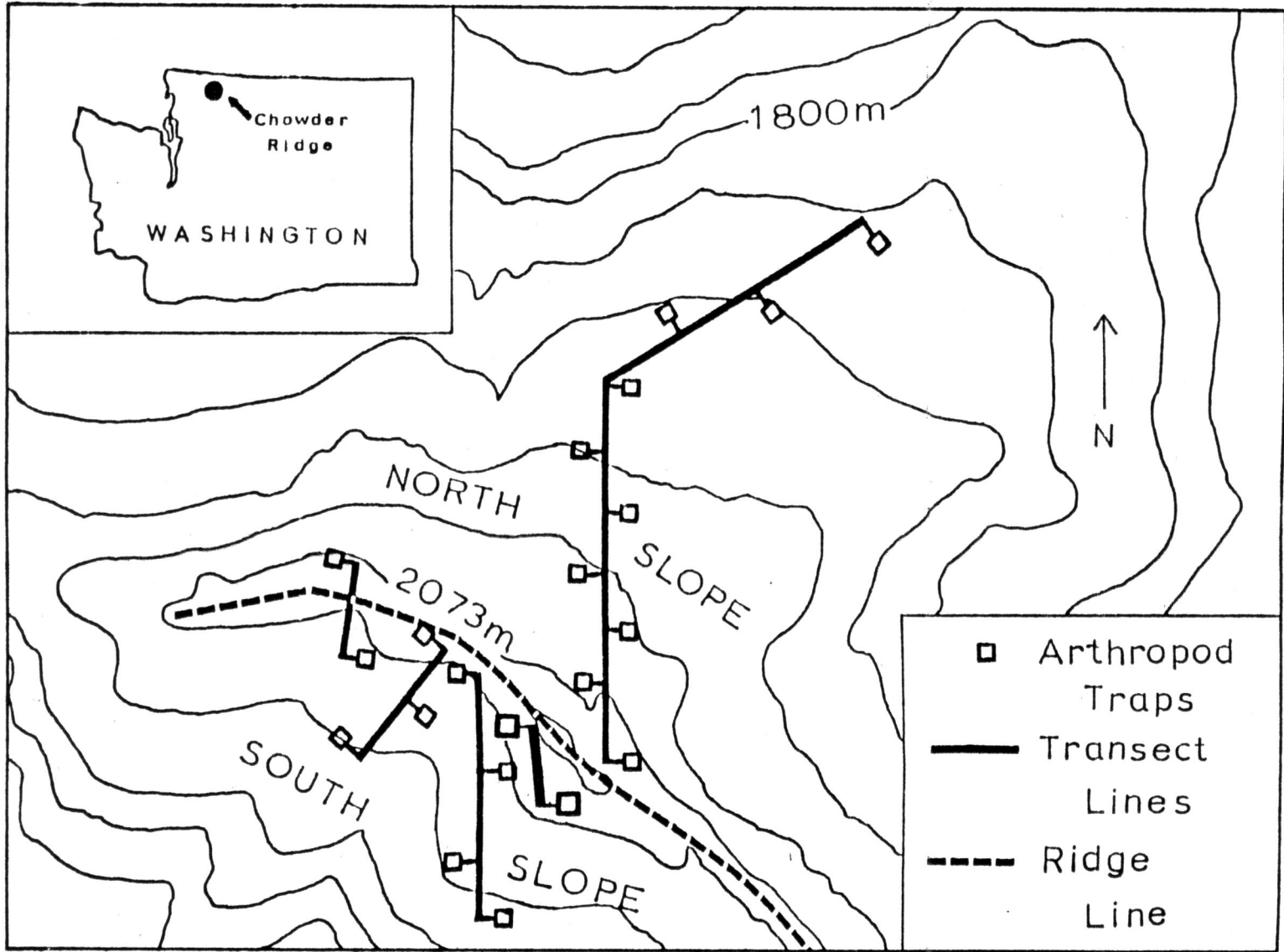
METHODS AND MATERIALS

Foraging locations and feeding behaviors of guild members were recorded on both snow covered and snowfree surfaces on both slopes. Arthropods were also collected on both slopes and surfaces.

Foraging Sites: It was assumed that frequency of occurrence per unit time (rather than numbers per unit area) was not only more pertinent to determining where birds foraged, but more feasible considering the steep, rugged topography and extreme variations in weather conditions on the ridge. Bird censuses were conducted along transect lines that were established on both slopes. Lines extended from the top of the ridge down each side to the ecotone between alpine and subalpine meadows, where the krummholz zone generally begins. Since the krummholz extends further up the south slope than up the north slope, one long line (approximately 1200 m) was established on the north slope and four shorter lines (approximately 72m, 144m, 216m, and 72m respectively) on the south slope (Fig. 1).

Nineteen censuses were conducted during the study period. Birds were recorded when actually in the census area or when entering or leaving. Species, number, cover (snow or snow-free), time, date, and slope were recorded. Care was taken to avoid double counting by excluding an individual when (a) it was seen or heard within 15 minutes and within about 30 m

Figure 1. Location of arthropod traps along avian census transect lines on Chowder Ridge.



of a previous sighting, or (b) it was observed continuously in the same area for any time period and was known to be the same bird.

A diurnal pattern of habitat use was recorded by carrying out censuses during different parts of the day. Census observations were divided into four time periods: morning (0700-1000 PST), midday (1001-1400 PST), afternoon (1401-1700 PST), and evening (1701-2000 PST). I did not spend equal amounts of time observing in each time period. Observations were pooled, and comparisons were made between snow covered and snowfree surfaces.

Cover (snowfree or snow cover) and slope (either north- or south-facing slope of the study area were the variables used in determining the foraging locations of guild members. Habitats (cover and slope) used as foraging sites were determined by:

- (a) measuring duration (in minutes) of the census period for each slope;
- (b) converting numbers of birds observed per minute to numbers observed per hour;
- (c) adjusting differences in area of snow in relation to snowfree cover on each slope (estimated average of 3% snow cover on the south slope and 90% snow cover on the north slope) and for changes in these differences due to snowmelt.

Foraging Behavior: The foraging rate (determined by counting the number of pecks per 10-second interval) of each

bird was recorded. An electronic metronome provided an audible reference interval. Pecks were categorized as "stationary" or "moving." "Stationary" pecks were defined as the number of pecks a bird made while remaining in one place during the 10-second interval. Pecks made while the bird walked, hopped, or ran were recorded as "moving." Data from these observations can be used to determine foraging rates and the percentage of time birds spent moving while foraging in each habitat.

Arthropod Sampling: Arthropod abundance and diversity were determined by collecting samples from snow covered and snowfree areas on both slopes along the same transect lines used during the avian census. Thus, samples were collected on both slopes from snow covered and snowfree areas, and at several elevations. Plastic potting trays (25.8 x 25.8 x 5.8 cm) were used as traps. The large surface area of each trap (665.6 cm²) allowed sampling of arthropod fallout as well as ground foraging forms. Traps used on snow were painted white, while those on vegetated areas were painted green. Each trap was set 10m on either side of the transect lines and marked with a numbered, yellow flag. Each trap was covered with a 2.5 cm mesh "chicken-wire" dome (height 13 cm), to deter large vertebrate predators. A water-detergent mixture in each trap served as a killing agent. Traps were placed on both slopes, and set in the ground or in snow so that the tops were flush with the surface. The first trap on each slope was placed at or near the crest of the ridge

with succeeding traps placed at a 30 to 31 m drop in elevation below the previous trap. A BM50 Precision Surveying altimeter was used to determine elevations (Fig. 1).

Arthropods were collected weekly for four weeks (collections totalled 78 trap-nights). Traps were cleared after being opened for 24 hours and the arthropods preserved in vials containing 70% ethanol. Vials were labelled with trap number, slope, date, and cover (snow/snowfree) (Table 1).

Weather Data: Air temperature, wind speed, and wind direction were recorded daily at a base camp on the lower north slope (elevation = 1890 m) at 0630 PST, 1630 PST, and 2000 PST.

Table 1. Collection dates and distribution of arthropod traps on Chowder Ridge.

| Collection Dates | North Slope | | South Slope | | Total Traps |
|--------------------------|-------------|----------|-------------|----------|-------------|
| | Snow | Snowfree | Snow | Snowfree | |
| July 18 | 9 | 0 | 1 | 7 | 17 |
| July 24 | 9 | 1 | 1 | 8 | 19 |
| August 1 | 8 | 3 | 1 | 9 | 21 |
| August 9 | 7 | 4 | 1 | 9 | 21 |
| Total (trap-nights) = 78 | | | | | |

RESULTS

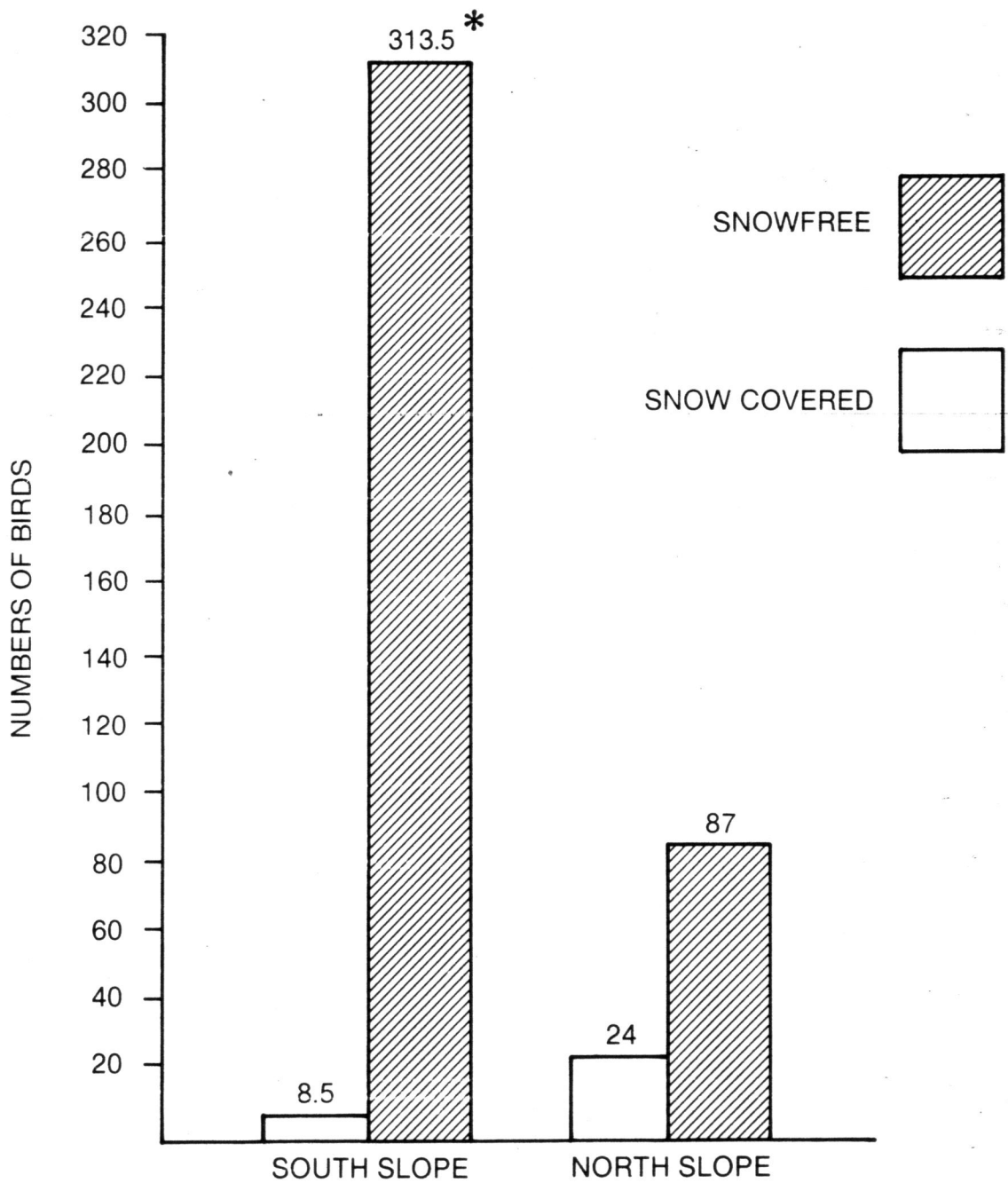
Foraging Sites: Birds were more common on snowfree surfaces than on snow covered surfaces (Two-Factor ANOVA; $F = 15.9$, $df = 1,18$, $p < 0.001$), and were found more frequently on the south slope than on the north slope (Two-Factor ANOVA; $F = 5.4$, $df = 1,18$, $p < 0.05$) (Fig. 2 and Tables 2 and 3). In addition, the interaction between slope and surface was highly significant (Two-Factor ANOVA; $F = 31.7$, $df = 1,18$, $p < 0.001$). Thus, the difference in use of snow and snowfree surfaces depended upon which slope the birds foraged.

There were consistently more birds on snowfree than on snow covered surfaces and on the south rather than the north slope throughout the observation period (Figs. 3 and 4). The daily averages of birds on snowfree and snow covered surfaces were 21 and 2 respectively; and for the south slope and north slope, 17 and 6 respectively.

Bird use of snowfree surfaces across all four time periods were significantly different compared to that for snow covered areas ($X^2 = 26.2$, $df = 3$, $p < 0.001$). Snowfree surfaces were used more frequently during the morning and mid-day; less frequently during the afternoon and evening. In addition, birds were found in greater numbers on snowfree surfaces than on snow during each time period (Table 4).

Foraging Behavior: Foraging behavior on snow covered and snowfree surfaces was measured by recording pecks per 10-

Figure 2. Total numbers of birds observed in relation to snow and snowfree surfaces and slope aspect.



* When a bird was encountered on both snow and snowfree surfaces during a single observation, it was recorded as 0.5 for each category.

Table 2. Occurrence of ground-foraging guild species in relation to snow cover and slope.

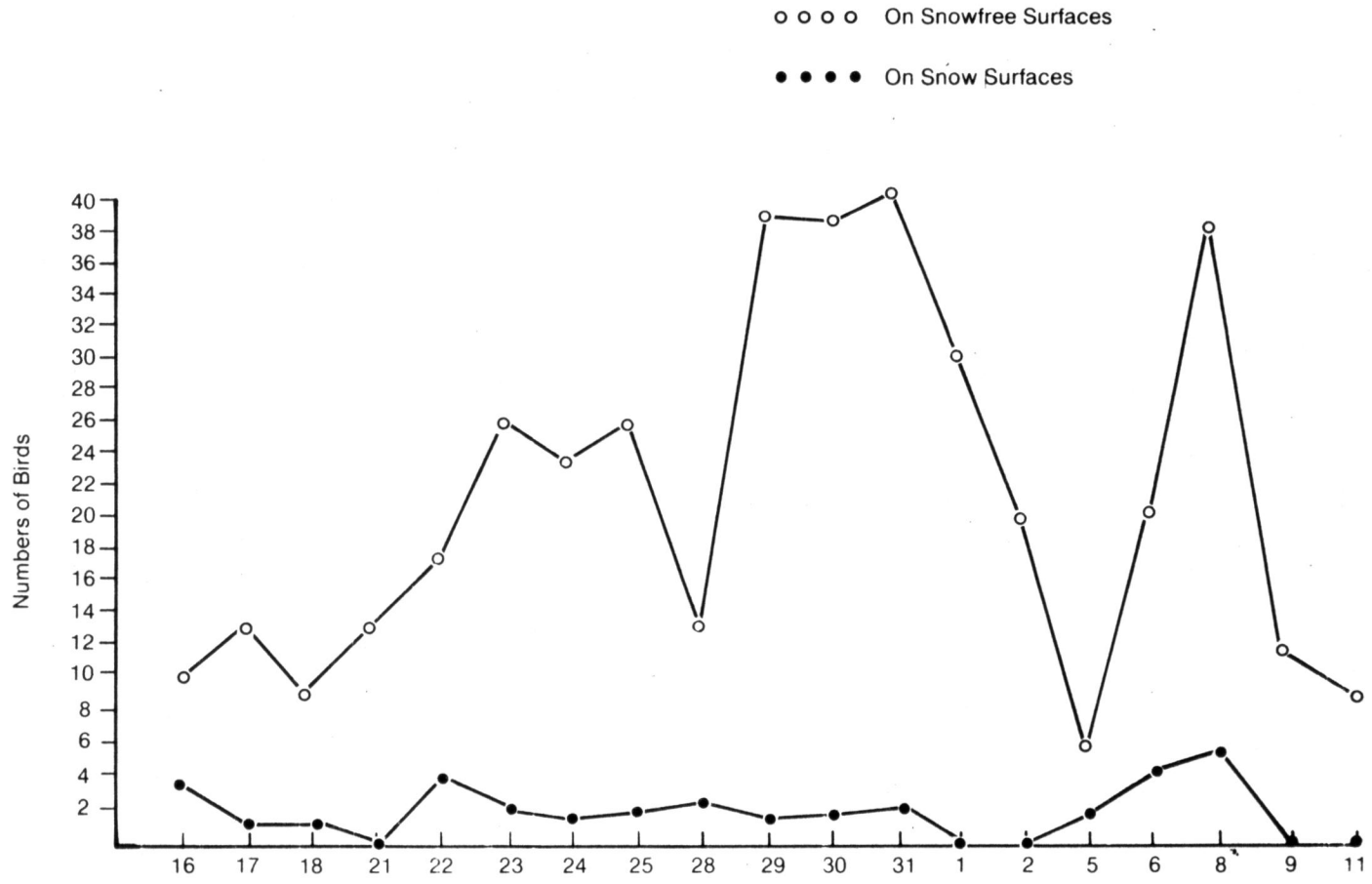
| Slope: | <u>Guild Members</u> | | | | | | Totals |
|----------|--------------------------|-------|----------------------------|-------|----------------------------|-------|--------|
| | <u>Rosy Finch (N=17)</u> | | <u>Water Pipit (N=202)</u> | | <u>Horned Lark (N=214)</u> | | |
| | North | South | North | South | North | South | |
| Cover:* | | | | | | | |
| Snow | 1 | 0 | 13.5 | 5.5 | 9.5 | 3 | 32.5 |
| Snowfree | 6 | 10 | 49 | 134 | 32 | 169.5 | 400.5 |
| Totals | 7 | 10 | 62.5 | 139.5 | 41.5 | 172.5 | |

*When a bird was encountered on both snow and snowfree surfaces during a single observation, it was recorded as 0.5 for each category.

Table 3. Summary for two factor analyses of variance for bird occurrence in relation to snow cover and slope.

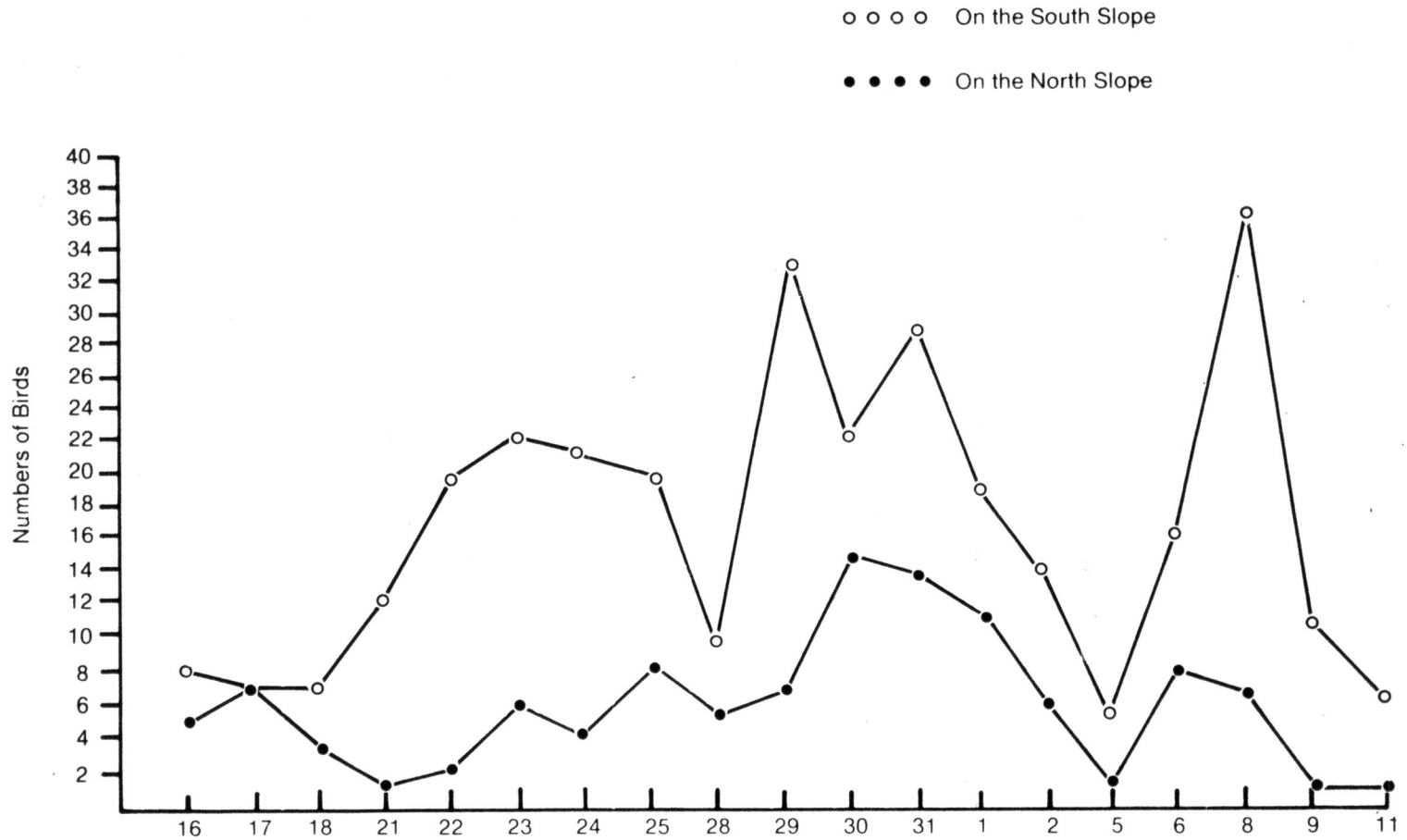
| Source | df | SS | MS | F | P |
|--------------------------|----|--------|-------|--------|------|
| Cover (Snow/Snowfree) | 1 | 9.892 | 9.892 | 15.853 | .001 |
| Error | 18 | 11.224 | 0.624 | | |
| Slope (North/South) | 1 | 3.044 | 3.044 | 5.416 | .030 |
| Error | 18 | 10.115 | 0.562 | | |
| Cover and Slope | 1 | 9.846 | 9.846 | 31.659 | .000 |
| Error | 18 | 5.605 | 0.311 | | |
| Within | 57 | 49.726 | | | |

Figure 3. The distribution of birds in relation to the presence or absence of snow cover.



JULY, AUGUST
SAMPLING PERIODS

Figure 4. The distribution of birds in relation to slope aspect.



JULY, AUGUST
SAMPLING PERIODS

Table 4. The diurnal frequency of birds on snow covered and snowfree surfaces.

| Time Period | Snow Surfaces | | | | Snowfree Surfaces | | | | Totals: Snow/Snowfree |
|--------------------------|---------------|----------------|----------------|-------|-------------------|----------------|----------------|-------|--------------------------|
| | Rosy Finch | Water Pipit | Horned Lark | Total | Rosy Finch | Water Pipit | Horned Lark | Total | |
| Morning (0700-1000) | 1 | 2.5* | 1 | 4.5 | 8 | 65.5 | 85 | 158.5 | 163 |
| Midday (1001-1400) | - | 7 | 3.5 | 10.5 | 6 | 77 | 82.5 | 165.5 | 176 |
| Afternoon (1401-1700) | - | 6 | 2 | 8 | 3 | 25 | 18 | 46 | 54 |
| Evening (1701-2000) | - | 5 | 4.5 | 9.5 | - | 9 | 21.5 | 30.5 | 40 |
| Totals | 1 | 20.5 | 11 | 32.5 | 17 | 176.5 | 207 | 400.5 | 433 |

*When a bird was encountered on both snow and snowfree surfaces during a single observation, it was recorded as 0.5 for each category.

second interval, (converted to pecks per minute), for Horned Larks and Water Pipits. Rosy Finches were never observed foraging on snow surfaces and only occasionally on snowfree areas. Larks and pipits foraged more frequently on snowfree surfaces and more sequences were recorded while they were there. Pipits foraged at a faster rate on snow (21 pecks per minute) than they did on snowfree surfaces (5 pecks per minute). Larks, on the other hand, foraged at a higher rate on snowfree surfaces (8 pecks per minute) than on snow (3 pecks per minute). Rosy Finches averaged 5 per minute on snowfree. Differences in rates between pipits and larks were significant on snow ($X^2 = 61.0$, $df = 1$, $p < 0.001$) and on snowfree surfaces ($X^2 = 75.8$, $df = 1$, $p < 0.001$) (Table 5).

Neither larks nor pipits made stationary pecks while on snow. Instead, they walked rapidly and steadily as they foraged over the snow surface. However, on snowfree surfaces both species periodically stopped and pecked at an object several times before moving. A comparison of the foraging tactics of the two species showed that larks devoted a larger percentage of time to stationary pecking than did pipits. (Table 6).

Arthropod Sampling: A total of 2602 arthropods, representing 17 orders, were collected from the snow covered and snowfree surfaces of both slopes during the four collecting days. Arthropods were identified to the familial level ex-

Table 5. Pecking rates of guild members on snow covered and snowfree surfaces.

| Guild Members | Snow Surfaces | | Snowfree Surfaces | |
|-----------------------------------|---------------|------------|-------------------|------------|
| | N | Pecks/min. | N | Pecks/min. |
| Rosy Finch | 0 | 0 | 9 | 5 |
| Water Pipit | 21 | 21 | 37 | 5 |
| Horned Lark | 21 | 3 | 123 | 8 |
| Totals (Pipits and Larks only) | 42 | 12 | 160 | 7 |

N = number of 10-second observations

Table 6. Pecking rates: stationary and moving (expressed as percentage of foraging time) for Water Pipits and Horned Larks.

| | Water Pipit | | Horned Lark | |
|------------|-------------|----------|-------------|----------|
| | Snow | Snowfree | Snow | Snowfree |
| Stationary | 00.00 | 11.00 | 00.00 | 42.00 |
| Moving | 100.00 | 89.00 | 100.00 | 58.00 |
| Totals | 100.00% | 100.00% | 100.00% | 100.00% |

cept for Lepidoptera (all were Microlepidoptera), Geophilomorpha and Lithobiomorpha (members of the class Chilapoda), and three orders of Arachnida. Dipterans were the most commonly captured order (41%). Arachnids (27.2%), homopterans (10.7%), and coleopterans (6.6%) were also frequently found (Table 7).

The numbers of arthropods increased with each collection. This trend was observed for the north and south slopes and for snowfree surfaces. In contrast, numbers of arthropods from snow covered surfaces decreased after the first collection and then increased with the fourth (Fig. 5).

The 78 trap-nights were used to compute expected values for arthropods for comparison of snow and snowfree surfaces and north and south slopes. Fifty-three percent of the traps were on snowfree surfaces, while 47% were on snow covered surfaces. Expected numbers for each surface were calculated as 1379 for snowfree surfaces and 1223 for snow covered surfaces. However, 2292 individuals were collected from snowfree surfaces and only 310 from snow. Arthropod numbers from these two surfaces were significantly different ($\chi^2 = 1286$, $df = 3$, $p < 0.001$). Numbers of arthropods collected from the north slope versus the south slope were also significantly different. Since 47% of the traps were on the south slope, the expected value would be 1223 individuals. However, 2153 individuals were captured. Although 1379 individuals were expected on the north slope, only 449 individuals were collected ($\chi^2 = 1334$, $df = 3$, $p < 0.001$).

Table 7. Percent composition, total numbers, and numbers of identified families for arthropod samples.

| Orders | Percent Composition | Total Numbers | Numbers of Families |
|----------------|---------------------|---------------|---------------------|
| Diptera | 41.16 % | 1071 | 24 |
| Acari | 12.22 | 318 | * |
| Homoptera | 10.76 | 280 | 5 |
| Araneida | 10.72 | 279 | * |
| Coleoptera | 6.62 | 172 | 10 |
| Collembolla | 4.57 | 119 | 4 |
| Opiliones | 4.34 | 113 | * |
| Hymenoptera | 3.80 | 99 | 8 |
| Hemiptera | 3.19 | 83 | 5 |
| Thysanoptera | 1.27 | 33 | 1 |
| Lepidoptera | 0.99 | 26 | * |
| Orthoptera | 0.12 | 3 | 1 |
| Trichoptera | 0.08 | 2 | 1 |
| Plecoptera | 0.04 | 1 | 1 |
| Siphonaptera | 0.04 | 1 | 1 |
| Geophilomorpha | 0.04 | 1 | * |
| Lithobiomorpha | 0.04 | 1 | * |
| Totals | 100.00 % | 2602 | 61 |

* Not keyed to family

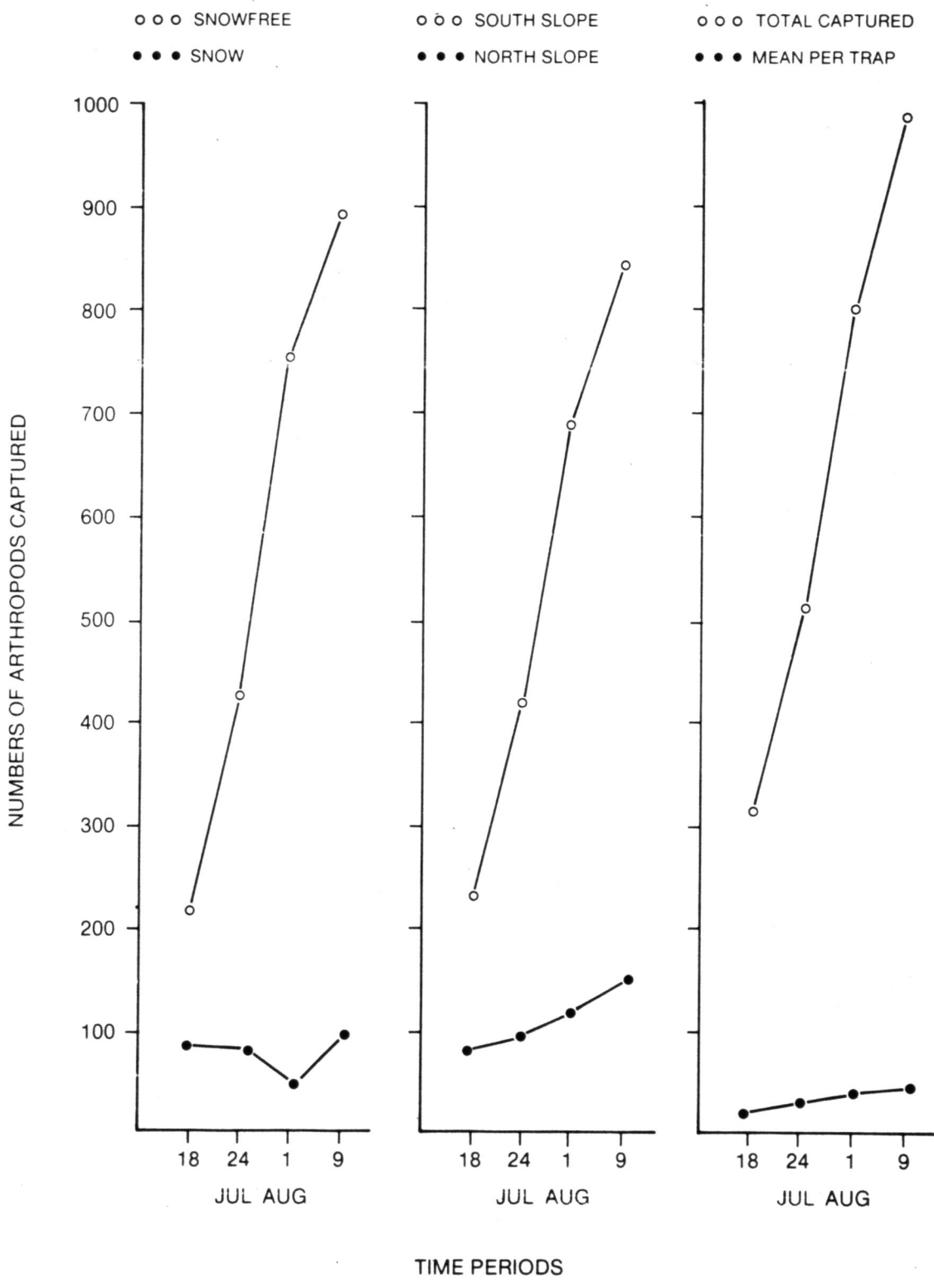


Figure 5. Numbers of arthropods captured: on snow/snowfree surfaces; total; mean per trap.

Numbers of arthropods per trap (as a measure of relative density) also increased dramatically with each weekly collection: 18.2 (18 July), 26.9 (24 July), 38.1 (1 August), and 46.7 (9 August). The mean number per trap was different on each surface (55.9 for snowfree and 8.4 for snow cover) for the four samples ($X^2 = 33.9$, $df = 3$, $p < 0.001$) (Table 8).

For slope, the difference was equally dramatic. The mean number of arthropods per trap was 10.9 for the north slope and 58.2 for the south slope ($X^2 = 33.5$, $df = 3$, $p < 0.001$).

Arthropods per m^2 were estimated from a ratio of the number of individuals per trap. These values (computed for surface cover and slope) are presented in Table 9.

Birds feeding in alpine and arctic tundra are selective in terms of size of prey items (Conry 1978, Seastedt and MacLean 1979). Therefore, a comparison of arthropod lengths from snow cover and snowfree surfaces should be useful. These averages were calculated using nine of 15 arthropod orders. Orders were excluded if their numbers were very small or if they were found only on one slope or on one type of surface. On snow covered surfaces the mean length was 3.3, mm and on snowfree areas mean length was 3.6 mm. The mean length of arthropods from the south slope was 3.7 mm, while those from the north slope were 3.4 mm (Table 10). These data were not treated statistically because a test of mean lengths between snow covered and snowfree surfaces or between north and south slope would not reveal large differences in numbers for each order.

Table 8. Relative densities of arthropods (mean numbers per trap) in relation to snow cover and slope.

| | Collection Dates | | Total Collected | Snow | | Snowfree | | North Slope | | South Slope | |
|-----------------------------|------------------|----|-----------------|-------|-----------------------|----------|-----------------------|-------------|-----------------------|-------------|-----------------------|
| | | | | N | \bar{X}/trap | N | \bar{X}/trap | N | \bar{X}/trap | N | \bar{X}/trap |
| Numbers of Arthropods | July | 18 | 310 | 86 | 8.60 | 224 | 32.00 | 84 | 9.33 | 226 | 28.25 |
| | July | 24 | 511 | 85 | 8.50 | 426 | 47.33 | 97 | 9.70 | 414 | 26.89 |
| | August | 1 | 801 | 47 | 5.22 | 754 | 62.83 | 119 | 10.82 | 682 | 68.20 |
| | August | 9 | 980 | 92 | 11.38 | 888 | 68.38 | 149 | 13.55 | 831 | 83.10 |
| Totals | | | 2602 | 310 | 8.38 | 2292 | 55.90 | 449 | 10.95 | 2153 | 58.19 |
| | | | | (12%) | | (88%) | | (17%) | | (83%) | |
| | | | E=1223 | | | E=1379 | | E=1379 | | E=1223 | |

E = Expected frequency values computed in relation to percentage of traps

Table 9. Relative Densities of Arthropods (per m²/24 hr)

| Snow Covered | | | Snowfree | | |
|----------------|----------------|-------|----------------|----------------|--------|
| South Slope | North Slope | Total | South Slope | North Slope | Total |
| 120.19 | 89.75 | 92.22 | 957.45 | 836.16 | 836.23 |

Table 10. Mean lengths of arthropod samples (in mm) for snow/snowfree surface and slope.

| Orders | Snow | | Snowfree | | North Slope | | South Slope | |
|----------------|------|-----------|----------|-----------|-------------|-----------|-------------|-----------|
| | N | \bar{X} | N | \bar{X} | N | \bar{X} | N | \bar{X} |
| Diptera | 153 | 4.9 | 918 | 2.8 | 158 | 4.7 | 896 | 2.7 |
| Araneida | 4 | 5.0 | 211 | 4.4 | 50 | 3.9 | 165 | 4.6 |
| Homoptera | 59 | 2.2 | 190 | 2.6 | 57 | 2.3 | 182 | 2.6 |
| Coleoptera | 23 | 5.0 | 124 | 9.6 | 38 | 6.0 | 106 | 10.1 |
| Hymenoptera | 14 | 3.2 | 77 | 4.0 | 17 | 2.8 | 71 | 4.1 |
| Hemiptera | 3 | 5.3 | 80 | 3.5 | 2 | 5.0 | 80 | 3.5 |
| Acari | 5 | 1.0 | 288 | 2.0 | 36 | 2.2 | 257 | 1.9 |
| Collembolla | 38 | 1.4 | 72 | 1.5 | 50 | 2.0 | 59 | 1.4 |
| Thysanoptera | 2 | 2.0 | 31 | 2.0 | 1 | 2.0 | 32 | 2.0 |
| Totals(N)* | 301 | | 1991 | | 409 | | 1848 | |
| Weighted Mean | | 3.8 | | 3.8 | | 3.8 | | 3.2 |
| Unweighed Mean | | 3.3 | | 3.6 | | 3.4 | | 3.7 |

* Totals will not equal total arthropods captured (Table 7) since not all specimens could be measured. Also, some orders were excluded due to very low sample sizes or to their absence on snow covered surfaces or from one of the slopes.

The diversities of arthropods on both snow covered and snowfree surfaces were calculated using the Shannon-Weiner function.

$$H = - \sum p_i \log_e P_i$$

This index was used to determine changes in the number of orders present and changes in the pattern of distribution of individuals among orders. The comparisons were made for both snow covered and snowfree surfaces for each sampling day. A distinctly higher diversity existed for snowfree surfaces ($t = 7.2$, $p < 0.01$) (Table 11).

Weather Data: Temperature and wind measurements were taken daily during the field study. Sunny and warm conditions prevailed during the day, with frequent afternoon clouds. Nights were cool, but dry. An afternoon thunderstorm occurred on 1 August, and cloudy conditions prevailed on 21 July, and 5 and 6 August. Steady fog, drizzle, and wind throughout the day of 7 August prevented data collection.

Base camp temperatures averaged 8.7°C for mornings (range 8°C to 14°C), 15.2°C for afternoons (range 11°C to 22°C), and 9.2°C for evenings (range 8°C to 11°C). Wind velocity for mornings, afternoons, and evenings averaged 5.2 mph (range 4 to 10 mph), 5.6 mph (range 3 to 10 mph), and 5.2 mph (range 0 to 9 mph) respectively. Winds were predominantly from the southwest.

Table 11. Diversity Indices (H) for Arthropods

| | | <u>Snow Surfaces</u> | <u>Snowfree Surfaces</u> |
|--------|----|----------------------|--------------------------|
| July | 18 | 1.34 | 1.87 |
| July | 24 | 1.24 | 1.94 |
| August | 1 | 1.37 | 1.72 |
| August | 9 | 1.42 | 1.92 |

DISCUSSION

With the exception of French (1959), Johnson (1965), and Verbeek (1967), there have been few studies which presented evidence of foraging patterns for alpine passerines. Although these investigators focused primarily on life histories and breeding patterns of Rosy Finches, Water Pipits, and Horned Larks, they did provide secondary consideration of foraging strategies in alpine habitats. In this study I focused on foraging patterns of these guild members and recorded their occurrence and use of two habitat surface covers: snow and snowfree. Both covers are essentially one-dimensional, or nearly so in the case of alpine vegetation zones (plants rarely grow more than 15-20 cm in height except in lower regions of the alpine zone).

Foraging Sites: Since guild members clearly foraged more frequently on snowfree areas, one would expect that these birds would use alpine meadows on the south slope rather than the north, particularly since southern exposures were mostly free of snow cover by early summer. The distinction between the birds' selection of snowfree areas of the south slope and their selection of snowfree areas of the north slope is significant. The vegetated and rocky "islands" that gradually emerge from retreating snow on the north slope form a patchy affect in an otherwise homogeneous environment. These patches seemed to be more attractive to birds than the few white patches of snow on the south slope.

These darker snowfree areas serve as localized regions of concentrated food sources, separated by areas of lower density food sources. This pattern is similar to that described by Morse (1970). Arthropod densities and abundances support this view for patch affect for the alpine snow/snow-free pattern.

Birds concentrated their foraging efforts on these snow-free patches of higher prey density, but continued to exploit areas of low prey density (snow), although at lower frequencies. This type of foraging behavior will permit birds to continually sample the environment in order to monitor changes in prey availability (Smith and Sweatman 1974, Smith and Dawkins 1971). Regular surveillance by predators of foraging areas, even those of low prey densities, may provide long-term benefits by allowing predators opportunities to optimize the food supply when it is at its lowest density (Thompson et al. 1974). I suggest that these alpine birds are monitoring the snowfields not only for the few conspicuous prey but also for a periodic "bonanza" of arthropods swept up from lower elevations by winds. Therefore, it is not the "snowpatch", but rather the snowfree "islands" of the north slope which are providing patches of more abundant prey.

Census data suggested there were optimal foraging periods for guild members. Higher frequencies (81%) of birds observed on snowfree surfaces during the morning and midday

periods may be due to the fact that 60% of total observation time was spent on the primarily snowfree south slope. About three fourths of the south slope observation time was during the morning and midday periods. Data are insufficient to determine if arthropod abundances were also greater during these two time periods for the south slope.

Foraging Behavior: Water Pipits displayed higher pecking rates than Horned Larks, a behavior supported by Verbeek (1970) and Edwards and Banko (1976). Pipits also had a higher pecking frequency on snow than on snowfree surfaces. Verbeek found a similar pattern for pipits, although peck rates were much higher (43/min. on snow, 7.8/min. on vegetated surfaces). However, the lower rates for larks on snow in this study were quite different from Verbeek's who calculated 38.3/min. for those birds on snow and 21/min. on snowfree surfaces. Edwards and Banko studied behavior patterns of foraging arctic tundra birds and recorded rates of 31.7/min. for pipits and 18.5/min. for larks on snow surfaces. I observed that on snow, pipits and larks move rapidly from one food item to another. Among vegetation, these birds walk slowly, frequently pecking at a potential food item from a stationary position. These observations agree with those of Verbeek (1970).

Despite their lower relative densities on snow, the contrast of arthropods on light background might enable birds to forage more efficiently (Verbeek 1970). This may be especially true when warm weather brings an influx of arth-

thropods as fallout onto snow surfaces. These influkes of arthropods make foraging on snow covered areas more "cost effective."

Birds rarely foraged on snow for more than a minute. These short foraging bouts may have been due to (a) the bird's vulnerability to predators on snow surfaces and/or (b) the negative thermal effects on the bird's body of prolonged exposure to a cold surface. The loss of a body heat may necessitate shorter feeding times on snow, especially when food sources are scarce.

While vegetated areas may house greater densities of arthropods, their accessibility is made difficult by the diversity of vegetational structure and complex niche arrangements. This may explain why birds move more slowly through vegetated areas.

Arthropod Sampling: The use of pitfall traps provides a relative, rather than an absolute, method for determining arthropod densities (Southwood 1966), and interpretations of population estimates and comparisons between habitats should be made cautiously. C. J. Norment (Washington State University, Pers. Comm.) proposed the use of a combination of sticky board and pitfall traps to optimize arthropod sampling for use in determining relative abundance of adult arthropods in tundra habitats. Sticky boards capture more dipterans and pitfall traps capture more ground beetles and spiders. Use of pitfall trays with wide surface areas may have provided a rea-

sonable compromise in that my samples cover a wide range of arthropod orders. Lepidopterans and orthopterans were probably the only significant prey of this avian guild that were underrepresented in the samples.

Dipterans were the largest component of the samples and are usually significant, if not dominant constituents among alpine and arctic tundra arthropods, especially on snowfields (MacLean and Pitelka 1971, Edwards and Banko 1976, Conry 1978, Norment pers. comm.). Mani (1968) reports that dipterans are the most numerous wind-borne arthropods on Himalayan snowfields.

The rapid increase in total arthropod numbers and densities with each sampling date suggests a peak in arthropod biomass no sooner than the middle of August. While my data are insufficient for correlating a peak abundance of arthropods with a peak in avian nesting activity, pipits were still in late stages of the nesting cycle in late July and early August. Eggs had just begun hatching in one pipit nest on the north slope during the first week of August and young were in another nest on the south slope as late as 9 August.

The higher frequencies of occurrences of birds on snow-free areas is correlated with arthropod abundance. Birds foraged where arthropods were most abundant. Soft-bodied forms (such as spiders and dipterans), important in nestling diets, make up a significant part of the summer diet of pipits (Schmoller 1968, Conry 1978). These groups were far

more abundant in the snowfree areas.

Arthropod lengths were thought to be helpful in determining what proportion of prey would be in the preferred size categories. Conry (1978) found that mean lengths of prey selected by alpine larks and pipits in Colorado were 7.90 mm and 8.05 mm respectively, and rarely were those of less than 2 mm or more than 16 mm selected. Mean lengths in my samples were 3.3 mm for snow and 3.6 mm for snowfree surfaces. This may be misleading since Conry's samples were taken not only from sticky boards but also from the gullets of nestlings. Samples from Chowder Ridge represent what may have been available as prey and ~~not what was~~ selected as prey. Arthropods composing the principal prey of larks and pipits were spiders, orthopterans, dipterans, lepidopterans, and homopterans (Conry 1978). These same orders in my samples had mean lengths ~~which were well within~~ those selected by larks and pipits in Conry's study. Future studies of alpine birds of Chowder Ridge may show correlations between prey selection by this guild and prey availabilities.

Determination of diversity indices for arthropods provided another way of comparing prey abundances on snow and snowfree habitats. Results of this analysis indicate that snowfree surfaces offered a wider variety of prey items, and that the difference when comparing both habitat surfaces is significant. Predictions could, therefore, be supported for more intensive foraging on these snowfree areas by this guild.

Weather Data: Temperature and wind patterns were so consistently mild throughout the study period that effects on bird and arthropod activity are thought to be negligible.

Number of birds recorded on 5 August were depressed, due perhaps to an atypical day (i.e., atypical for the study period) of dense fog, drizzle, and wind. Similar but even more inclement weather conditions on 7 August closed down all investigations on the study area and consequent effects on birds and arthropods was unknown.

SUMMARY

The summer foraging patterns of alpine Rosy Finches, Water Pipits, and Horned Larks, were investigated to determine how these passerine members of a ground-foraging guild utilize snow surfaces and snowfree areas for feeding. Avian censuses determined frequency of occurrence for these two habitat covers. Relative prey abundances were determined as well as bird foraging behavior on snow and snowfree surfaces.

This study was conducted on Chowder Ridge, in the Mt. Baker-Snoqualmie National Forest in Washington from 11 July through 9 August, 1984. One hundred and forty-six hours were spent on observation and collection. Data on weather conditions were collected on a daily basis.

Conclusions made from the results of this study are:

1. The alpine passerine guild selected snowfree habitats more often than snow surfaces for foraging purposes.
2. Since the south slope of the ridge is predominately snowfree most of the summer, the guild utilizes this slope to a much greater extent than it does the north slope.
3. The difference in bird utilization of snowfree areas on the north slope was much more significant than the difference in use on the south slope. Birds were selecting snowfree "islands" on the snow covered north slope as "patches" of high prey density.
4. The relative density and diversity of arthropods were considerably greater on snowfree surfaces. Such abun-

dances may make prey more available to foraging guild members despite the fact that arthropods may be more difficult to locate in the complex plant structures of snowfree areas.

5. Despite lower arthropod densities and diversities on snow surfaces of the ridge, birds continue to monitor such areas for potential conspicuous food items and for changes in prey densities.

6. Bird foraging behavior differences between the two habitats reflected a more rapid pecking rate on snow, with a quicker, more steady pace than on vegetated areas. Search time was less on this homogeneous surface for numbed prey which are conspicuous and easily captured. The rate of movement and pecking on vegetated areas was slower, with frequent pauses, required by the birds' constant searching and probing among clumps of vegetation for a more dense yet less conspicuous prey. When prey densities become temporarily high on snow, foraging efficiency should be more nearly maximized than it would be for snowfree areas.

7. Arthropods, whose size and taxa were most preferred by alpine passerines, have greater relative densities on the snowfree areas and on the warmer south slope rather than on snow surfaces.

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APPENDIX

The following list includes numbers of arthropods for each family (or superfamily) in relation to snow covered (SC) and snowfree (SF) surfaces for each collection.

| | 18 Jul | | 24 Jul | | 1 Aug | | 9 Aug | |
|-----------------|--------|----|--------|-----|-------|-----|-------|----|
| | SC | SF | SC | SF | SC | SF | SC | SF |
| DIPTERA | | | | | | | | |
| Sciaridae | 2 | 17 | 3 | 111 | 1 | 91 | 4 | 73 |
| Cecidomyiidae | | 2 | | 4 | | 122 | 1 | 68 |
| Anthomyiidae | 12 | 4 | 4 | 3 | 3 | 12 | 13 | 46 |
| Mycetophilidae | 2 | 1 | 13 | 2 | 8 | 6 | 4 | 7 |
| Chironomidae | 3 | | | 14 | | | 1 | 5 |
| Phoridae | 3 | 1 | 2 | 7 | 3 | 22 | | 27 |
| Tipulidae | | 14 | | 5 | | | | 1 |
| Ephydriidae | 1 | 2 | 1 | | | | 1 | |
| Chloropidae | 1 | | | 1 | | 9 | | 92 |
| Dolichopodidae | | 2 | | 2 | | 3 | | 8 |
| Muscidae | 2 | | | 1 | 5 | 18 | 14 | 6 |
| Elephariceridae | | 1 | 10 | | | | 3 | |
| Heleomyzidae | | | | 1 | | | | |
| Empididae | | | 1 | 4 | 1 | 72 | 5 | 54 |
| Sphaeroceridae | | | | 1 | | | | |
| Ceratopogonidae | | | | 1 | 1 | 4 | | |
| Syrphidae | | | | 1 | 1 | 1 | | |
| Tachinidae | | | | 1 | | | | 2 |
| Therevidae | | | | | | 2 | | |

APPENDIX - Continued

| | 18 Jul | | 24 Jul | | 1 Aug | | 9 Aug | |
|-----------------|--------|----|--------|----|-------|----|-------|----|
| | SC | SF | SC | SF | SC | SF | SC | SF |
| DIPTERA (Cont.) | | | | | | | | |
| Drysophilidae | | | | | | 5 | | |
| Calliphoridae | | | | | | 1 | | |
| Canaceidae | | | | | | | | 3 |
| Pipunculidae | | | | | | | | 1 |
| Agromyzidae | | | | | | | | 1 |
| HOMOPTERA | | | | | | | | |
| Aphididae | 35 | 1 | 3 | 4 | 6 | 6 | 13 | 12 |
| Cicadellidae | 1 | 12 | 1 | 23 | 2 | 37 | 2 | 79 |
| Psyllidae | 1 | 1 | 2 | 1 | 2 | | 2 | 1 |
| Chermidae | | | | | 1 | | 1 | |
| Coccoidea | | 1 | | 21 | | 2 | 1 | |
| COLEOPTERA | | | | | | | | |
| Staphylinidae | 1 | 3 | 2 | 1 | 1 | 5 | 1 | 2 |
| Scarabaeidae | 1 | 8 | | 23 | | 14 | 1 | 10 |
| Chrysomelidae | | 1 | | | | 3 | | |
| Elateridae | 1 | 3 | | 5 | | 5 | | 1 |
| Carabidae | 2 | 1 | 3 | 10 | 1 | 31 | 3 | 12 |
| Coccinellidae | | 1 | 2 | 3 | | | 1 | |
| Scolytidae | | | | 1 | | | | |
| Leptinidae | | | | 1 | | 1 | | |
| Derrestidae | | | | | | 1 | | 1 |

APPENDIX - Continued

| | 18 Jul | | 24 Jul | | 1 Aug | | 9 Aug | |
|--------------------|--------|----|--------|----|-------|----|-------|----|
| | SC | SF | SC | SF | SC | SF | SC | SF |
| COLEOPTERA (Cont.) | | | | | | | | |
| Thylacitinae | | | | | | | 1 | |
| COLLEMBOLA | | | | | | | | |
| Isotomidae | 2 | 6 | 25 | 6 | 8 | 5 | 3 | 46 |
| Entomobryidae | | 3 | | 6 | | | | |
| Poduridae | 1 | | 1 | | | | | 4 |
| Sminthuridae | | | | | | 2 | | 1 |
| HYMENOPTERA | | | | | | | | |
| Mymaridae | | 2 | | 2 | | 1 | | |
| Tenthredinidae | | 4 | | 2 | | 1 | 2 | 1 |
| Formicidae | | 2 | | 4 | | 4 | | 3 |
| Ichneumonidae | 1 | | | 3 | 1 | 4 | 1 | 6 |
| Xiphydriidae | | | | 1 | | | | |
| Braconidae | | | | 3 | | 14 | 1 | 12 |
| Cynipidae | | | | | | 1 | | |
| Chalcidoidea | 4 | 2 | 2 | 2 | | 2 | 3 | 8 |
| HEMIPTERA | | | | | | | | |
| Miridae | | 2 | | 2 | | 13 | 1 | 24 |
| Tinsidae | | | | 5 | | 12 | | 4 |
| Saldidae | | | | 1 | | | | |
| Pentatomidae | | | 1 | | 1 | | | |

APPENDIX - Continued

| | 18 Jul | | 24 Jul | | 1 Aug | | 9 Aug | |
|-------------------|--------|----|--------|----|-------|----|-------|----|
| | SC | SF | SC | SF | SC | SF | SC | SF |
| HEMIPTERA (Cont.) | | | | | | | | |
| Lygaeidae | | | | | | 17 | | |
| THYSANOPTERA | | | | | | | | |
| Thripidae | | | | 1 | | 2 | 1 | 29 |
| ORTHOPTERA | | | | | | | | |
| Acrididae | | | | 1 | | 1 | | 1 |
| PLECOPTERA | | | | | | | | |
| Leuctridae | | | | | | 1 | | |
| TRICHOPTERA | | | | | | | | |
| Hydroptylidae | | | | | | 1 | | |