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FORAGING OF HORNED LARKS AND WATER PIPITS IN ALPINE COMMUNITIES

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Abstract.—Snowfields are reported to improve the foraging efficiency of Horned Larks (*Eremophilia alpestris*) and Water Pipits (*Anthus spinoletta*) breeding in alpine zones (the snowfield hypothesis). We counted larks and pipits in snow and snow free communities of Chowder Ridge in the Mt. Baker-Snoqualmie National Forest, Washington. We found little support for the snowfield hypothesis. Both species more frequently occurred in snow free communities than on snow (94.5% of the time for larks, 89.9% for pipits). Larks most commonly (63.7%) foraged in dry, sparsely vegetated, fell-field communities. Pipits foraged in more different communities and more mesic habitats than larks. Snow free areas yielded a greater diversity of arthropods and more arthropods/trap-day compared to snow. If larks and pipits did forage on snow, they did so late in the afternoon after updrafts from lower elevations deposited insects on the snow.

FORRAJEO POR PARTE DE *EREMOPHILIA ALPESTRIS* Y *ANTHUS SPINOLETTA* EN COMUNIDADES ALPINAS

Sinopsis.—Se ha informado que los campos cubiertos con nieve mejoran la eficiencia de forrajeo de individuos de *Eremophilia alpestris* y *Anthus spinoletta* que se reproducen en zonas alpinas (hipótesis de los campos-de-nieve). Determinamos el número de individuos de ambas especies en comunidades cubiertas o nocubiertas de nieve en Chowder Ridge y el Parque Nacional del Monte Baker-Snoqualmie, Washington. Nuestros datos le ofrecen muy poco apoyo a la hipótesis de los campos-de-nieve. Encontramos con muchísima mayor frecuencia a ambas especies en comunidades sin nieve. La alondra (*E. alpestris*) se observó forrajeando mayormente (63.7% de las ocasiones) en comunidades secas con vegetación esparcida. Por su parte, *A. spinoletta* se observó forrajeando en diferentes comunidades y en habitats más mésicos que los que utiliza la alondra. Las áreas desprovistas de nieve proveyeron de una mayor diversidad de artropodos y de una mayor frecuencia de capturas/día que las áreas cubiertas con nieve. Cuando ambas especies forrajean en áreas cubiertas de nieve, tienden a hacerlo bien entrada la tarde cuando las corrientes de aire de elevaciones bajas han depositado en la nieve insectos.

Passerines confront a contrasting pattern of snow and snow free areas when exploiting alpine habitats. This pattern forms a horizontal mosaic of nesting and foraging sites, and birds may select territories based on the presence or absence of snow. For example, nests have been described as located near snow banks and early summer foraging as occurring on or at the edges of snow (Braun 1980, Conry 1978, Pattie and Verbeek 1966, Verbeek 1970).

Verbeek (1970) emphasized the importance of snow (the snowfield hypothesis) by concluding that species having snowfields within their territories have an advantage when hunting for food. Observations that bodies of chilled and dead, wind-blown arthropods often litter snowfields support this hypothesis (Edwards 1972, 1987; Edwards and Banko 1976; Mani 1962, 1968). To test the snowfield hypothesis, we censused Horned Larks (*Eremophilia alpestris*) and Water Pipits (*Anthus spinoletta*) in several alpine communities. Our goals were to find where larks and pipits foraged relative to snow cover and to compare food available on snow and snow free surfaces.

Insectivorous birds may favor snowfields if such areas have (a) greater densities of arthropods compared to snow free areas, or (b) higher availability of arthropods because of increased conspicuousness of prey items on snow surfaces compared to snow free areas. Because birds often forage where the feeding rate is highest (Goss-Custard 1981), comparison of foraging behavior of alpine passerines relative to snow may show if snow surfaces do increase efficiency and if birds are feeding in the most profitable habitats.

STUDY AREA

We studied larks and pipits during the summer of 1984 on Chowder Ridge (48°49'N, 121°51'W) in the Mt. Baker-Snoqualmie National Forest, Washington. The ridge, at the northwest base of Mt. Baker, extends from the northwest to the southeast, and divides the study area into north and south facing slopes. Both slopes are steep, and extensive snowfields and a glacier cover much of the north facing slope. Elevation along the ridge varies from 2032 m to 2313 m. Variable diurnal and seasonal temperatures, frequent precipitation, intense radiation and westerly winds characterize Chowder Ridge (Douglas and Bliss 1977).

Taylor and Douglas (1978) and Douglas and Bliss (1977) described the alpine plant communities on Chowder Ridge and in the Mt. Baker region, respectively. Snow covered approximately 3% of the south slope and 90% of the north slope during this study.

METHODS

We counted larks and pipits down transect lines on either slope from the ridgetop to the alpine-subalpine meadow ecotone. We recorded species, numbers, and associated community where sighted (snow, dwarf shrub, herb-field, fell-field, vegetation stripe and krummholz). Although plant communities were sharply delineated, we did not precisely determine the area of each community transected by census lines. Therefore, our data describe "use" of habitat and not "selection" of habitat in the sense of use vs. availability (Alldredge and Ratti 1986, Johnson 1980). Since time and energy generally limit habitat use (Levins 1968), occupation indicated to us use of that habitat. We alternated censuses among four periods (all Pacific Daylight Time): early morning (0700–1000), late morning (1000–1300), early afternoon (1300–1600) and late afternoon (1600–1900). Each slope had the same number of census stations, and we kept numbers of censuses equal for all time periods.

We recorded birds' foraging rates as pecks/10 s interval. Pecks were either "stationary" (pecks made at the same place during the 10 s interval) or "moving" (pecks made while walking or running).

Along the same transect lines, we used plastic potting trays (25.8 × 25.8 × 5.8 cm) as arthropod traps (painted white if placed in snow or green if placed in snow free areas). At ca. 30 m drops in elevation, we placed traps flush with the surface, covered them with a 2.5 cm wire-mesh dome (ht = 13 cm), and used a water-detergent mixture as a killing agent. The traps' large surface area (665.6 cm^2) allowed sampling of both fallout and terrestrial arthropods. We collected for a 24 h interval weekly for 4 wk (approximately 1900 trap-hours). After preserving arthropods in 70% ETOH, we identified collections to superfamily or family (Norvell 1985), and calculated diversity (H') (Shannon and Weaver 1949).

RESULTS

Occurrence and distribution.—If snow provides a foraging advantage to alpine passerines, we predict that larks and pipits occur more commonly on snow than on snow free surfaces. Yet, we observed both species significantly less often on snow than on snow free areas (Kolmogorov-Smirnov Test, D = 0.98, df = 1, $P < 0.05$; Table 1). Hendricks (1987) also reported that Water Pipits used snowfields less than vegetated areas.

Larks and pipits occupied snow or snow free habitats at significantly different times (Kolmogorov-Smirnov Test, D = 0.61, df = 15, $P < 0.01$; Table 2). Birds were more abundant in snow free areas during the early and late morning, and more abundant on snow in mid- and late afternoon periods.

We found that each species had significantly different community associations (Kolmogorov-Smirnov Test, D = 0.83, df = 4, $P < 0.01$). Larks more commonly occurred in fell-field communities, sparsely vegetated sites along the ridgetop. Pipits occupied a wider range of communities than larks and were in more mesic, less exposed sites. Braun (1980), Drury (1961), Hendricks (1987), and Verbeek (1970) report similar microsite differences for these species.

Arthropod sampling.—Traps on snow free surfaces caught most of the insects (88.1%, n = 2606), contained a greater diversity (t-test, $t_{(1,9)} = 2.17$, $P < 0.05$) and significantly more arthropods/trap-day (t-test, $t_{(1,9)} = 3.05$, $P < 0.05$). All traps captured a wide range of arthropodan orders (n = 16), representing both resident and aerial dispersers (Edwards 1987). Average size of captured arthropods was not significantly different between trap surface locations (Kolmogorov-Smirnov Test, D = 0.51, df = 8, $P < 0.05$; Table 3). Arthropods captured/trap increased with each collection, and differences captured in snow free traps vs. snow traps became more pronounced with each sampling period.

Foraging behavior.—Larks and pipits had significantly different foraging rates on the two surfaces (Mann-Whitney, $z = 6.9$, $P < 0.0001$). Pipits averaged 21.6 (±12.6) pecks/min on snow and 5.4 (±3.2) pecks/min on snow free areas, whereas larks had 3.0 (±1.4) pecks/min on snow and 8.6 (±7.9) pecks/min on snow free surfaces. Neither species made

Table 1. Number of Horned Larks and Water Pipits seen on snow and snow free surfaces.

	Surface			
	Snow		Snow free	
Species	*n*	%	*n*	%
Larks	11	(5.5)	190	(94.5)
Pipits	20	(10.1)	178	(89.9)
Totals	31	(7.8)	368	(92.2)

stationary pecks while on snow, although both larks and pipits periodically stopped and pecked at one location when foraging in snow free habitats.

DISCUSSION

Because Verbeek (1970) found territories of Water Pipits and Horned Larks associated with areas of snow accumulation, he concluded that foraging in snowfields was advantageous to these species. Censuses, foraging observations, and arthropod samples from our study do not support this "snowfield hypothesis." Our evidence is that the comparatively lower resource level in snow provides less available food for larks and pipits. This conclusion is consistent with results from other alpine areas (Hendricks 1987).

We found larks and pipits in alpine communities similar to those recorded by Conry (1978), Drury (1961), and Verbeek (1967, 1970), suggesting that these species use consistent cues when choosing territories. Larks were in drier sites with shorter vegetation, pipits in wetter sites with taller vegetation. Community characteristics also may explain the observation that pipits' territories consistently had snow somewhere within their boundaries (Verbeek 1970). As snow melted, sites would be more hydric with taller vegetation. Pipits may not select territories for the snow bank itself, but for the vegetation that the melting snow provided.

Conry (1978) and Verbeek (1967, 1970) have identified summer diets of larks and pipits, and we did not investigate prey use. Instead, we focused on what prey items were available on the two surfaces. Alcock (1973) and Royama (1970) suggested that birds search out and exploit certain foraging locations rather than look for specific prey items. We believe larks and pipits foraged in this way. Our trapping showed that there were many more arthropods available in snow free compared to snow areas. Additionally, differences in prey availability between snow free and snow covered became greater as the season progressed. Snow free areas were the major foraging locations for both species. Further, larks and pipits foraged more commonly in certain areas at certain times. Such behavior allows these species to exploit any heterogeneity of opportunity in the alpine, and represents a coarse-grain foraging response to their environment (Levins 1968). In this form of foraging, birds exploit the most profitable areas first, effectively establishing a hierarchy of for-

TABLE 2. Percent occurrence of Horned Larks and Water Pipits in alpine communities during different census periods.

	Census time period									
	0700–1000		1000–1300		1300–1600		1600–1900		Total	
Community Species:	Lark	Pipit	Lark	Pipit	Lark	Pipit	Lark	Pipit	Lark	Pipit
Snow	0.4	1.5	1.0	3.0	2.0	3.5	2.0	2.0	5.4	10.1
Fell-field	16.4	7.6	26.9	23.3	10.0	9.1	7.0	2.5	60.2	42.5
Herb-field	16.9	11.6	3.0	4.0	1.5	2.5	1.0	0.0	22.4	18.1
Dwarf shrub	5.5	13.6	1.5	3.6	3.0	4.0	1.5	5.6	11.5	26.8
Vegetation stripe	0.5	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.5	1.5
Krummholz	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.5	0.0	1.0
Totals (%)	39.8	35.8	32.4	34.2	16.5	19.1	11.5	10.6	100	100
n	80	71	65	68	33	38	23	21	201	198

TABLE 3. Numbers and mean lengths of arthropod orders captured in traps on snow and snow free habitats.

Habitat:	Snow		Snow free	
Order	*n*	x̄ Length (mm)	*n*	x̄ Length (mm)
Acari	5	1.0	288	2.0
Araneida	4	5.0	211	4.4
Coleoptera	23	5.0	124	9.6
Collembola	38	1.4	72	1.5
Diptera	153	4.9	918	2.8
Hemiptera	3	5.3	80	3.5
Homoptera	59	2.2	190	2.6
Hymenoptera	14	3.2	77	4.0
Thysanoptera	2	2.0	31	2.0
Others	18	3.3	124	3.4

aging locations. For example, larks and pipits may switch from primary, snow free areas to snow as a way of monitoring transient changes in prey availability. If significant "fallout" had not occurred, birds would quickly return to snow free communities.

When would larks and pipits ever forage on snow? Although both species foraged more frequently and for longer duration in snow free patches, snowfields may provide an occasional and temporary bonanza of prey items. When we observed larks and pipits on snow, it was in early and late afternoon. Then, updrafts from lower elevations were most likely carrying up and depositing arthropods on snow (Spalding 1979). Under these conditions, snow surfaces would be energetically more profitable than adjacent snow-free areas (Spalding 1979). Prey also may be somewhat immobilized by the colder surface temperature of snow and may be more conspicuous against the white background. Although not used as primary foraging areas, it may be advantageous for larks and pipits to monitor snowfields for potential prey bonanzas.

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