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Foraging ecology of alpine-nesting water pipits Anthus spinoletta

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FORAGING ECOLOGY OF ALPINE-NESTING WATER PIPITS, *ANTHUS SPINOLETTA*

by

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ABSTRACT

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Foraging Ecology of Alpine-nesting Water Pipits, *Anthus spinoletta* (67 pp.)

Director: Richard L. Hutto RLH

The foraging ecology of alpine-nesting Water Pipits, (*Anthus spinoletta*), was studied during the summers of 1983 and 1984 on the Beartooth Plateau (3200 m elevation) in Park County, Wyoming. Most observations were concentrated on six nesting pairs. The study was designed to investigate patterns of (1) habitat use, and (2) foraging behavior of pairs with nestlings.

Alpine terrain was divided into four habitat types: tundra meadow, fellfield, snowfield, and "other." Prey availability scores (prey encounters/m traveled) were significantly greater ($P < 0.001$) for snowfields than for tundra meadow or fellfield habitats. However, adult pipits tended to visit tundra meadow sites more often than expected, and snowfields less often than expected. The contradictory results can be explained by examining data on arthropod distributions and sizes found in the habitats and comparing these with the kinds of arthropods delivered to nestlings. A large proportion (64.8%) of the arthropod biomass delivered to the nestlings was comprised of organisms (lepidopteran caterpillars, pupae, and adults, millipedes, and large spiders) never sampled on snowfields and that were larger than the kinds found on snow. Water Pipits forage most where they have the greatest probability of encountering preferred sizes and types of prey.

Parental investment (measured by number of deliveries to nestlings, fecal sac removal, and time spent incubating and brooding) was not useful in predicting patterns of sexual niche partitioning of foraging space by pairs of Water Pipits. Distribution of the orientation of trip departures from nests was significantly different between pair members in all cases. The mechanism(s) maintaining this pattern of spatial segregation is not known, but may be the result of female dominance during the breeding season. Delivery rate of food to nestlings was positively correlated to nestling age. There was a concurrent positive correlation between delivery rate and percent of foraging trips <50 m from the nest. Adult pipits flew significantly longer distances from nests when departing with fecal sacs. This is probably an adaptation to reduce the probability of nest detection by predators, and represents a trade-off between energy-efficient foraging and reproductive success.

ACKNOWLEDGMENTS

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CHAPTER ONE

INTRODUCTION

When first encountered, alpine regions appear simple in structure. They lack the three dimensional complexity of forests, and they seem to lack the vegetative diversity found in other biomes, even such places as deserts. While it is true that alpine regions are comparatively simple with relatively low species diversity, they are not uniform in structure. Even a brief glance reveals a variety of major habitat components, such as boulderfields, snowfields, and tundra. Nevertheless, the very fact of the "simplified" nature of the component habitats makes alpine areas ideal sites for investigating various patterns of distribution, dispersal, and habitat use of the organisms found there.

The chapters that follow explore two aspects of foraging ecology of an alpine-nesting passerine bird, the Water Pipit (*Anthus spinoletta*). In the first chapter I examine the patterns of habitat use by nesting pairs of pipits on foraging trips. I test a long-standing hypothesis that snowfields are an important source of arthropod food ("fallout") for nesting alpine birds. In the second chapter I examine several variables that may influence how adult pipits forage when tending nestlings. In particular, I determine whether or not sexual niche partitioning exists in a simple environment where division of space becomes more difficult; I examine how the age of nestlings influences distances foraged from the nest and the frequency of food deliveries to the nestlings; and I examine how the pipits may modify the efficiency of their foraging activities around the nest in order to reduce the probability of their nestlings being detected and killed by predators.

CHAPTER TWO

HABITAT USE BY ALPINE-NESTING WATER PIPITS: A TEST OF THE SNOWFIELD HYPOTHESIS

A substantial quantity of arthropods is deposited in alpine areas as fallout (Mani, 1962, 1968; Swan, 1967; Edwards, 1972, 1973; Edwards and Banko, 1976; Papp, 1978; Spalding, 1979; Mann et al., 1980), and is especially noticeable on surfaces of summer snowfields. A variety of scavengers and predators use arthropod fallout on alpine snowfields for food (Mann et al., 1980), including several bird species (Pattie and Verbeek, 1966; Edwards and Banko, 1976). Pattie and Verbeek (1966) speculated that snowfields may be important habitat as a source of food for alpine insectivorous birds, implying that the ease with which snow surface arthropods are detected and captured should make them a frequently used resource. This intriguing hypothesis was expanded and investigated by Verbeek (1970), who noted that foraging rates of water pipits (*Anthus spinoletta*) and horned larks (*Eremophila alpestris*) were much greater on snow than off, leading Verbeek (1970) to suggest that it would be advantageous for an alpine nesting bird to have a portion of a snowfield within its territory, thereby reducing energy expended when hunting for food. Verbeek's (1970) snowfield hypothesis has been echoed and/or supported by Edwards (1973), Hoffmann (1974), Edwards and Banko (1976), and Braun (1980).

However, Verbeek's (1970) hypothesis remained untested.

I examined the habitat use-availability relationship of nesting pairs of pipits at the time they were feeding nestlings, when the demands for food were greatest and considerable energy was being expended by foraging adults. In this paper I (1) test the validity of Verbeek's snowfield hypothesis, (2) provide a general description of habitat use by nesting pipits, and (3) present an explanation for the pattern of habitat use observed.

STUDY AREA

The study area was the same as that used by Verbeek (1970) on the Beartooth Plateau, Park County, Wyoming, just below Beartooth Pass, at about 3200 m elevation. I centered my study site around the large, permanent snowfield at the base of "Pipit Hill" (Verbeek, 1970). This area encompassed four principal habitat types upon which the following analysis is based. The first type, alpine tundra, corresponded to Pattie and Verbeek's (1966) dry meadow association and was typified by ground cover of a variety of forbs and grasses. Maximum vegetation height was about 15 cm. The second type, fellfield, corresponded to Pattie and Verbeek's (1966) type of the same name. This type supported mostly cushion plants and scattered forbs, but was at least 40-50% rock and soil. While scattered forbs were as tall as 15 cm, most vegetation was less than 2 cm in height. The third type, snowfield, was essentially a two dimensional habitat of permanent and semipermanent snow. The fourth type, "other", encompassed rock outcrops, talus, and pond margins. Each component of the latter type was mostly without vegetation and snow. Additional descriptions of the site, and the Beartooth area in general, are provided by Johnson and Billings (1962), Pattie and Verbeek (1966), and Verbeek (1970).

METHODS

I searched for active water pipit nests in snow-free areas adjacent to the permanent snowfield on the study site during June-August of 1983 and 1984. My observations of foraging activities were concentrated on six focal nests, each 20-60 m from the nearest snow at the time eggs hatched. Nests 1 and 2 were observed in 1983, the remaining four in 1984.

Adult females of each of the six pairs were captured with a butterfly net while they were on their nests, banded with color bands and USFWS aluminum bands, and additionally marked with a dab of yellow acryllic paint on the back of the head. Adult males were not captured, but I am confident sex classification was accurate because only female water pipits incubate and brood (Verbeek, 1970). At each of the six nests only the color-marked bird incubated the clutch and brooded the nestlings.

Once eggs hatched at the six focal nests, I recorded where pipits traveled (along the nearest of eight principal compass directions) when adults departed the nest on foraging trips. I observed the nests with 9X binoculars from a position at least 60 m from each nest. At this distance the adults appeared undisturbed by my presence so long as I remained relatively inactive. I made observations throughout the daylight hours in 2-h sessions. Distances and directions traveled were recorded in reference to series of stakes placed at 20 m intervals for 40 m along the four cardinal directions around each nest. The farther a bird traveled, the greater became the error of the estimated distance traveled. To minimize this problem I paced distances from each nest to distant landmarks, to be used as reference points when making estimates of longer foraging trips. I also used distances between my stakes as a scale for foraging trips that were to points nearer the nests.

For each trip I recorded direction, distance traveled, and habitat visited only where foraging was first initiated. I made maps of total foraging areas for each pipit by plotting the point of the longest observed trip along each of the eight compass directions, and connecting these points to form a convex polygon around each nest. By weighing cutouts of these polygons and comparing them with the weight of a 1 ha cutout drawn on the same scale as the foraging area maps, I calculated foraging areas for each bird. Superimposing the outlines of the foraging area polygons on habitat maps of the study site provided a measure of the availability of each habitat type to each individual pipit.

I measured foraging rates and travel rates of pipits in each habitat with a stopwatch. Foraging rates were recorded (when possible) as the time required to take 20 pecks. I assumed each peck represented a prey encounter, and that a pipit pecked at prey items it determined were potentially capturable, whether or not they were captured. I did not include in this analysis observations of birds that were obviously pecking more than once at the same prey organism. Travel rates were recorded as the time required to traverse 5 m. From study skin measurements and observations of foraging pipits I estimated pipits covered 1 m in 15 strides. Since I could not record foraging and travel rates simultaneously, I recorded first the foraging rate and then the travel rate for each bird, making only one set of measurements for each bird per trip when recorded.

Prey availability scores for the three principle habitats (alpine tundra, fellfield, snowfield) were calculated using the equation:

$$A_i = F_i / T_i$$

where A_i = prey availability score of habitat i, F_i = foraging rate (pecks/min) of a pipit in habitat i, and T_i = travel rate (meters/min) of a pipit in habitat i. The scores obtained represent the number of prey encountered over a finite distance (1 m) of habitat that the foraging bird determines are capturable, i e., A_i represents a measure of available prey density.

Arthropods were not sampled in 1983. In 1984 I sampled arthropods in the three principal habitats. For alpine tundra and fellfield habitats the sampling routine was identical. Pairs of plastic drinking cups (6 cm in diameter), used for pitfall traps, were set flush with the surface of the ground at 10 stations in each of these habitats. These trap stations were checked for 18 consecutive days, and emptied daily when possible. I also made 240 sweeps with a sweep net in each of these habitat types, sampling each habitat equally each sampling day. Pitfall trap and sweep net samples were collected in the late afternoon. Using this routine I obtained a relative measure of the diversity and size distribution of arthropods in each of these two habitat types.

For arthropod sampling of snowfield habitat I randomly located five 1-m plots on the snow surface each sampling day by tossing a stake out on the snow and then placing a wire hoop to the S side of the point where the stake had landed. I collected all arthropods found on the surface within each of these plots. These samples were collected in late afternoon and early evening. This provided a measure of the actual arthropod diversity and size distribution for the snowfield habitat.

I sampled nestling foods using the pipe cleaner, neck ligature method (Johnson et al., 1980). Ligatures were left in place for a maximum of 60 min, and no brood was sampled more than once per day, usually in the morning. Food items recovered from nestlings (and snow surface samples) were preserved in 70% ethyl alcohol and analyzed in the laboratory.

Statistical analysis of habitat use by each pair of pipits followed Neu et al. (1974). Other statistical procedures used followed Sokal and Rohlf (1981), with significance levels set at 0.05.

RESULTS

HABITAT USE

Observed foraging areas for the six pairs of nesting water pipits ranged from 3.29 to 10.14 ha; the foraging areas of the 12 individual pipits ranged from 1.76 to 10.14 ha (Table 1). Pair members foraged often in areas visited infrequently or not at all by their mates (Hendricks, 1987), though foraging areas of pair members overlapped to varying degrees. Thus, the combined foraging areas presented in Table 1 are not simply the sums of the areas of mates. Each foraging area encompassed segments of all four habitat types. The frequency distributions of habitat use differed (G test for goodness of fit, df = 2, $P < 0.001$) from that expected on the basis of habitat availability for each of the six pairs. Snowfields were used less (Bonferroni's z statistic, $P < 0.05$) (Figure 1) than expected by each of the six pairs, one of the two vegetated habitats was used more ($P < 0.05$) than expected (alpine tundra in five cases, fellfield in one case). "Other" habitats, such as talus, rock outcrops, and pond margins were visited infrequently, and were used less ($P < 0.05$) than expected by two pairs (pairs 15 and 16)(Figure 1).

Habitat use by individuals of pairs was similar to habitat use by the pairs themselves. Frequency distributions of habitat use for all 12 individuals differed from expected (G test for goodness of fit, df = 2, $P < 0.001$ for all cases except male 9, where $P < 0.05$)(Table 2). For 11 of 12 cases snowfields were used less (Bonferroni's z statistic, $P < 0.05$) than expected, while alpine

Table 1. Observed foraging areas (ha) of nesting pairs of water pipits. Areas of mates overlap to various degrees.

Pair	Male	Female	Sexes Combined
1	7.54	2.56	8.88
2	10.14	2.21	10.14
7	4.89	6.63	7.95
9	3.68	2.58	4.63
15	1.76	3.10	3.29
16	3.50	4.75	5.50

Figure 1. Histograms of habitat use and availability for six nesting pairs of Water Pipits. Number in upper right corner of each set is the number of the nesting pair. Habitat type symbols are: T = alpine tundra, F = fellfield, S = snowfield, O = "other". A plus or minus means a habitat type was used more or less than expected, based on Bonferroni's z statistic.

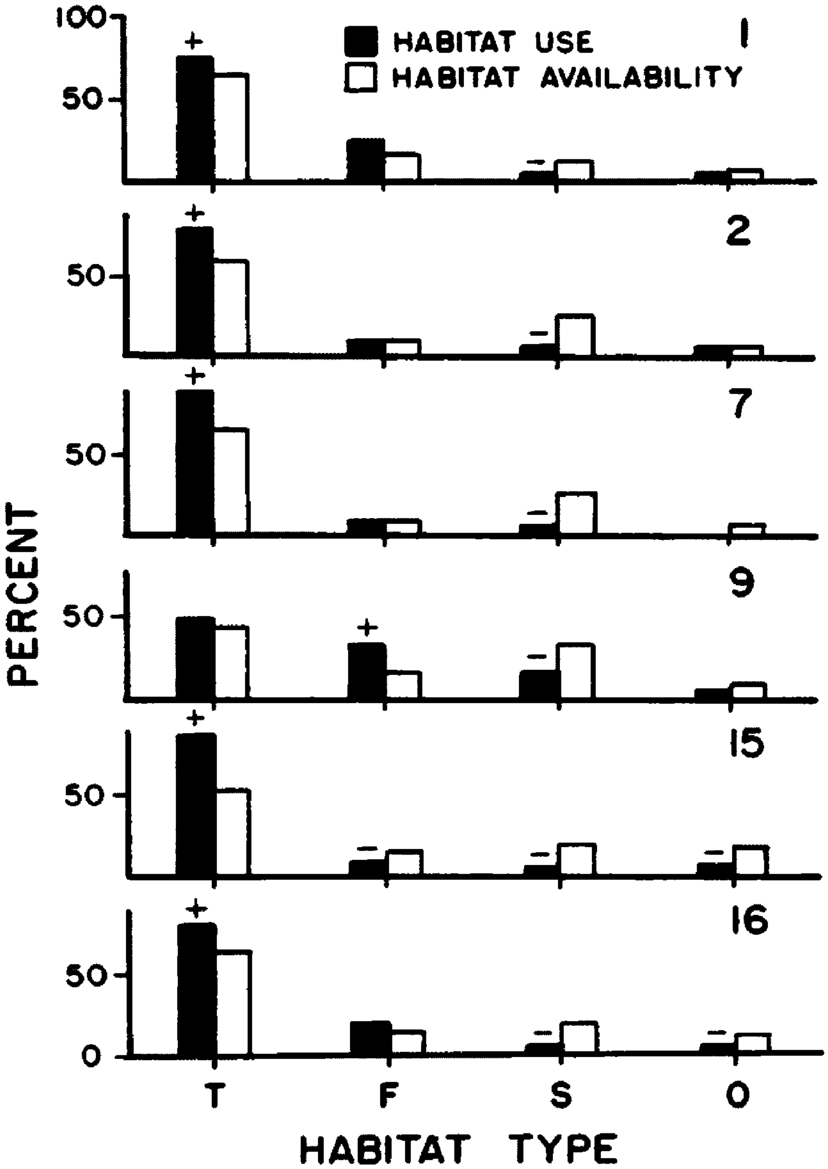
100
50
■ HABITAT USE
□ HABITAT AVAILABILITY
1
+
–
2
7
9
15
16
0
PERCENT
T
F
S
O
HABITAT TYPE

Table 2. Habitat use (number of visits) and availability for each water pipit (observed = O, expected = E). A plus or minus means a habitat type was visited significantly more or less than expected.

	Alpine Tundra		Fellfield		Snowfield		Other[a]		N	P[b]
	O	E	O	E	O	E	O	E		
Males										
1	110	90+[c]	13	23-[c]	3	15-	10	8	136	<0.001
2	312	239+	51	39	23	104-	14	18	400	<0.001
7	68	49+	5	5	1	18-	0	2	74	<0.001
9	43	37	18	14	17	25	1	3	79	<0.05
15	68	39+	5	10	0	13-	1	12-	74	<0.001
16	88	62+	12	12	1	18-	1	10	102	<0.001
Females										
1	222	208	91	54+	0	33-	0	18	313	<0.001
2	236	164+	17	27	5	71-	17	13	275	<0.001
7	38	29+	4	3	2	11-	0	1	44	<0.001
9	17	21	21	7+	4	14-	2	2	44	<0.001
15	91	57+	8	15	1	20-	9	17	109	<0.001
16	32	29	14	6	0	8-	2	5	48	<0.001

[a] rock outcrops, talus, pond margins.

[b] G test for goodness of fit, df = 2.

[c] based on Bonferonni's z statistic at $\alpha = 0.05$ (Neu et al., 1974).

tundra (eight cases) or fellfield (two cases) was used more ($P < 0.05$) than expected. For 10 of 12 cases, one of the vegetated habitats was used more ($P < 0.05$) than expected, based on availability. "Other" habitats were visited infrequently and usually in proportion to their availability in the foraging areas used by the adult pipits.

HABITAT USE AND TIME OF DAY

There was no apparent relationship between time of day and frequency of visits to snowfields by water pipits (Table 3). Rates of visitation to snow in morning, midday, and evening ranged from 0.0-0.75 trips/h for all pairs except pair 9, with rates of 1.83 and 2.22 trips/h in morning and midday, respectively. Rates of visitation to non-snowfield habitats during the three time periods ranged from 6.25-16.0 trips/h for all pairs.

PREY AVAILABILITY BY HABITAT

Snowfields had a larger (Mann-Whitney U test, $P < 0.001$) prey availability score ($\bar{X} \pm$ SE)(2.6 ± 0.2, N = 33) than either alpine tundra (1.9 ± 0.1, N = 61) or fellfield (1.3 ± 0.1, N = 26). The prey availability score of alpine tundra was larger (Mann-Whitney U test, $P < 0.01$) than the score for fellfield. Foraging rates ($\bar{X} \pm$ SD) along the pond margin exceeded those of snowfield (89.3 ± 29.9 pecks/min, N = 6 vs 37.0 ± 11.7 pecks/min, N = 61, respectively).

HABITAT SAMPLES OF ARTHROPODS

All arthropods sampled were classified to taxonomic group and

Table 3. Time of day and number of foraging trips to non-snow (N) and snowfield (S) habitats by water pipits on the Beartooth Plateau. AM, MD, and PM represent morning (0800-1200 MDT), midday (1230-1630), and evening (1700-2030), respectively.

	AM			MD			PM		
	N	S	h[a]	N	S	h	N	S	h
Pair									
1	131	1	10	129	0	10	186	2	15
2	251	8	16	182	9	12	214	11	23
7	47	1	4	43	0	4	25	2	4
9	64	11	6	38	10	4.5	--	--	--
15	91	1	6	67	0	6.5	24	0	1.5
16	125	1	12	24	0	3.5	--	--	--

[a] Observation time, in hours.

assigned to one of three size categories based on total length: <5 mm = 0, 5-10 mm = 1, and >10 mm = 2. Since alpine tundra and fellfield habitats were sampled identically, the results obtained for these two habitats are compared directly. Snowfield results are presented separately, since the sampling method was unique for that habitat.

I found no differences (R X C test of independence) between alpine tundra and fellfield habitats in size categories of arthropods sampled by either pitfall trapping ($G = 5.396$, $df = 2$, $P > 0.05$) or sweep netting ($G = 1.452$, $df = 2$, $P > 0.1$)(Table 4). Mean (± SE) size categories of arthropods collected in alpine tundra and fellfield habitats, respectively, were 0.953 ± 0.023 and 1.011 ± 0.032 for pitfall trapping, and 0.545 ± 0.035 and 0.462 ± 0.061 for sweep netting.

Spiders (Araneae) and beetles (Coleoptera) comprised 97.9% (41.6 and 56.3%, respectively) of the numbers of arthropods captured by pitfall traps in alpine tundra , and 99.6% (30.8 and 68.8%, respectively) of those captured by pitfall traps in fellfield (Table 4). In contrast, flies (Diptera) and true bugs (Hemiptera) comprised 78.8% (65.3 and 13.5%, respectively) of the numbers of arthropods captured by sweep netting in alpine tundra, and 87.9% (76.9 and 11.0%, respectively) of those captured by sweep netting in fellfield (Table 4).

The mean size category of arthropods sampled from the snowfield habitat was 0.141 ± 0.015. Flies, and aphids and leafhoppers (Homoptera) comprised 69.0% (36.0 and 33.0%, respectively) of the total numbers of arthropods sampled on the snowfield surface (Table

Table 4. Number of individual arthropods in each of 3 size classes (mm) in pitfall and sweep net samples from alpine tundra and fellfield.

	Alpine Tundra			Fellfield		
	<5	5-10	>10	<5	5-10	>10
Pitfall Traps						
Araneae	32	321	28	33	112	22
Coleoptera	218	126	172	112	134	127
Diptera	-	-	-	-	-	1
Hemiptera	-	1	-	-	-	-
Lepidoptera	-	-	1	-	-	-
Orthoptera	-	11	6	-	-	1
Subtotal[a]	250	459	207	145	246	151
Sweep Net						
Araneae	7	-	-	1	-	-
Coleoptera	-	1	-	-	-	-
Diptera	95	92	7	38	28	4
Hemiptera	26	14	-	9	1	-
Homoptera	20	-	-	-	-	-
Hymenoptera	4	10	-	5	4	-
Lepidoptera	-	2	-	-	1	-
Orthoptera	-	9	10	-	-	-
Subtotal[b]	152	128	17	53	34	4
Total	402	587	224	198	280	155

Table 4. (continued)

[a] $G = 5.396$, $df = 2$, $\underline{P} > 0.05$ comparing alpine tundra with fellfield pitfall trap results.

[b] $G = 1.452$, $df = 2$, $\underline{P} > 0.1$ comparing alpine tundra with fellfield sweep net results.

Table 5. Numbers of arthropods by size class (mm) sampled from snowfields (30 1-m^2 plots) on 6 days, June-August 1984.

	<5	5-10	>10
Araneae	1	1	-
Coleoptera	5	5	1
Diptera	191	34	2
Hemiptera	30	23	-
Homoptera	208	-	-
Hymenoptera	85	10	4
Lepidoptera	28	2	-
Total	548	75	7

5). Wasps and bees (Hymenoptera) accounted for an additional 15.7%.

Comparing across habitats, small arthropods (< 5 mm) comprised 33.1 and 31.3% of the samples in alpine tundra and fellfield, respectively, but represented 87.0% of the standing crop of individuals collected from the snowfield (Figure 2). Large arthropods (> 10 mm) comprised 18.5, 24.5, and 1.1% of the samples from the three habitats, respectively.

DAILY USE OF SNOWFIELDS BY WATER PIPITS

The maximum percent of daily foraging trips to snowfields by adult pipits was 18% in mid-July 1984 (Figure 3). This decreased to 10% and zero by late July. It was not greater than 2% of the total for any single day after 20 July. Peak visitation to snow corresponded approximately to maximum densities of snowfield arthropods ($31.8/m^2$). I was unable to sample snowfield arthropods and pipit foraging trips during a week in early July 1984 when foraging trips to snow, and snowfield arthropod densities, may have been greater than those recorded. For late July to early August, snowfield arthropod densities remained between $18.4-24.0/m^2$.

NESTLING FOODS

I obtained foods during 38 h of sampling of 5-11 day old nestlings at five nests in 1984. Mean (± SE) size of organisms (assigned to categories 0, 1, or 2) in the nestling food samples was 0.903 ± 0.053 (Table 6). Flies, true bugs , and moths (Lepidoptera) comprised 80.6% of the total number of organisms collected (58.3, 11.1, and 11.1%, respectively). Millipedes (Diplopoda) and a snail

Figure 2. Frequency distributions of size classes of arthropods sampled in 1984 from alpine tundra (T), fellfield (F), snowfield (S), and nestling foods (N). Size classes are based on total length. Numbers above bars are sample sizes. Methods of sampling are different, so direct comparison of all habitats is not possible.

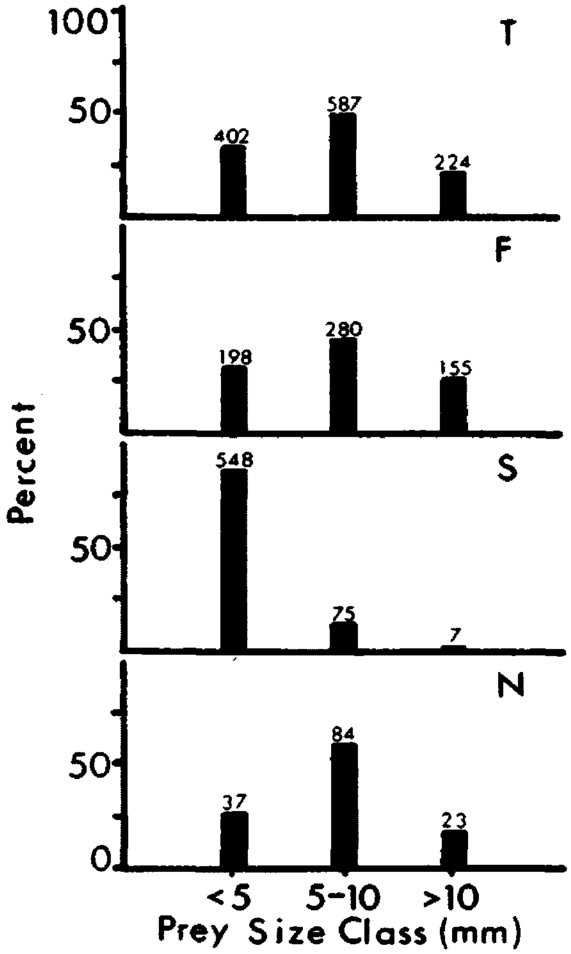
100
50
0
Percent
T
402
587
224
F
198
280
155
S
548
75
7
N
37
84
23
<5
5-10
>10
Prey Size Class (mm)

Figure 3. Proportion of daily foraging trips to snowfields by adult Water Pipits, and corresponding snow surface arthropod densities, Beartooth Plateau 1984.

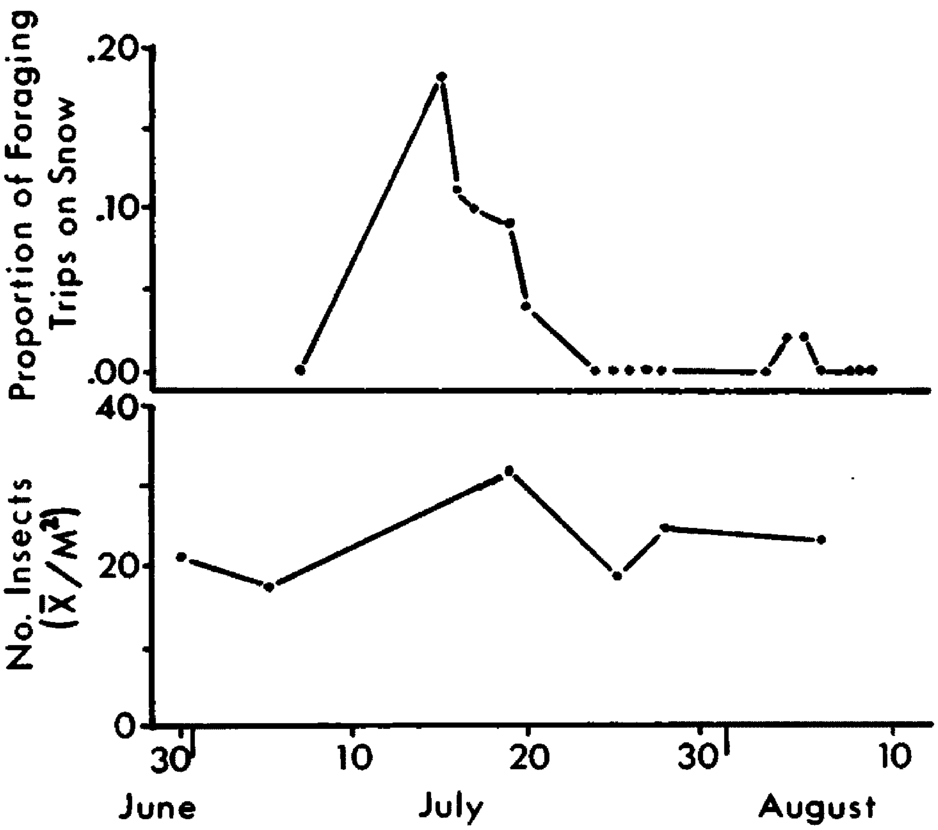
Proportion of Foraging Trips on Snow
.20
.10
.00
40
No. Insects ($\bar{X}$/M²)
20
0
30
10
20
30
10
June
July
August

Table 6. Food items by size class (mm) collected from nestling water pipits in 1984, based on 38 nestling hours of sampling at 5 nests.

	<5	5-10	>10
Araneae	-	-	1
Diplopoda	-	-	3
Coleoptera	-	3	-
Diptera	13	68	3
Hemiptera	6	10	-
Homoptera	15	-	-
Hymenoptera	2	2	1
Lepidoptera (adult)	-	-	5
Lepidoptera (caterpillar)	-	1	5
Lepidoptera (pupae)	-	-	5
Gastropoda	1	-	-
Total	37	84	23

(Gastropoda) occurred in the samples, although in relatively small proportions (2.1 and 0.7% of the total, respectively).

Small organisms (< 5 mm) comprised 25.7% of the food samples while large organisms (> 10 mm) comprised only 16.0% (Figure 2). Large organisms comprised 73.8% of the biomass of the samples.

While observing adult pipits foraging, I identified parts of 62 prey loads delivered to nests. Lepidopterans were identified on 44 (71.0%) of these deliveries, dipterans on 12 (19.4%), spiders on four (6.5%), and grasshoppers (Orthoptera) and flying ants (Hymenoptera) on one (1.6%) delivery each.

DISCUSSION

Pairs of water pipits on foraging trips visited snowfields significantly less often than expected, based on the proportion of that habitat lying within the boundaries of the foraging areas. Although pairs of pipits appeared to avoid visiting snowfields, there may be sex differences in habitat use (a form of niche partitioning) such that one sex may use snowfields preferentially. This possibility was not supported by the data (Table 1). Both members of the six pairs usually visited snowfields significantly less and alpine tundra or fellfield significantly more than expected. Thus, the snowfield hypothesis of Verbeek (1970) is not supported.

Verbeek (1970) based his conclusion about the relative importance of snowfields as sources of food on foraging rates (or pecks/min) of birds in different habitats. He observed foraging rates on snow to be more than 4 times as great as in vegetation. A better measure of prey availability, and of habitat importance, might be the frequency with which potential prey are encountered in both time and space. Prey availability scores obtained for the three principal habitats (alpine tundra, fellfield, and snowfield) at the Beartooth Plateau study site show that prey is more available (Mann-Whitney U test, $P < 0.001$) on snowfields than in the two other habitats. This supports Verbeek's (1970) observations and presents a paradox. Prey are most available in a habitat that is generally avoided by foraging pipits. There are at least three possible explanations for this pattern.

First, water pipits on snowfields are especially conspicuous to avian predators, such as prairie falcons (Falco mexicanus), and tend to avoid snow on this basis. I have no data to test this alternative. Pipits on snowfields are certainly more conspicuous to a human observer, and prairie falcons do attack and eat water pipits in the alpine (Marti and Braun, 1975; pers. observ.), but whether predation is important enough to select against snowfield foraging behavior is unknown.

Second, abundances of arthropods on snowfields are not uniform over time, such that there are flushes and times of relative scarcity (Edwards and Banko, 1976; Papp, 1978; Spalding, 1979). Water pipits may forage on the snow only during the flushes. Daily peaks in prey abundance seem likely, but water pipits showed no particular pattern of daily snowfield use (Table 3). Edwards and Banko (1976) also noted that no particular time period seemed to be preferred by snowfield foraging birds in Alaska. Weekly variation in arthropod abundance is also likely. For the Beartooth Plateau site I found densities of snowfield arthropods to range from 17.8 to 31.8/m^2. Peak bird activity on the snowfield corresponded roughly to the peak of arthropods on the snow (Figure 3). Edwards and Banko (1976) found that the greatest amount of bird activity on Alaskan snowfields (in mid-June) corresponded to highest densities of arthropods on the snow. However, density of arthropods on snowfields does not appear to be the complete explanation for predicting when, and how much, water pipits will forage on snowfields. Water pipit visitation (Figure 3) declined from 18% to zero during late July and early August, while densities of arthropods on the snow remained at about 19 to 24/m^2.

Third, there are significant differences in the sizes and types of arthropods found in different habitats. Water pipits foraged in habitats where they had the greatest probability of encountering preferred prey organisms. Water Pipits are generalist predators (Bent, 1950; Hayward, 1952; Gibb, 1956; this study), in that they feed on any organisms they encounter and can handle. However, though pipits are generalist predators, it still is advantageous for them to forage where net energy gains make it most profitable to do so. While snowfields harbor prey that is easy to locate and capture, it usually is not the kind of food that pipits seek for their offspring. Most of the largest prey items delivered to nestlings (lepidopteran pupae, caterpillars and adults, millipedes, and large spiders) (Table 6) were never sampled on snow (Table 5). Thus, pipits forage on snowfields only infrequently when raising young because the prey they prefer is elsewhere.

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CHAPTER THREE

FORAGING PATTERNS OF WATER PIPITS WITH NESTLINGS

For many bird species reproduction involves chosing a place in which to find a mate, nest, and raise young. During brood-rearing stages adult birds must not only find food for themselves while avoiding predators, they must also find food for their young and minimize the risks of predation upon their nestlings. Thus, one would expect natural selection to act strongly to influence where birds breed, and how they conduct themselves during the process of rearing offspring (Cody 1981). By examining how breeding birds deal with the immediate problems of acquiring food and avoiding predation we can gain useful insights into understanding how conflicting demands shape life history strategies (e.g., Ricklefs 1977).

Bird species in which both adults participate in raising young face an additional complication with regard to foraging. Male and female parents living in the same limited space may compete for food. If depression of food resources is a possible consequence of foraging, coexisting predators (in this case, parents of the same species) may minimize competition by (1) hunting for different subsets of the prey resource, (2) using different foraging behaviors, (3) hunting at different times, and (4) hunting in different places (Charnov et al. 1976). Division of resources in each of these ways has been documented for pairs of nesting birds (e.g. Selander 1966, Robins 1971, Power 1980, Knapton 1984a).

Like most other alpine-nesting birds, Water Pipits (*Anthus* spinoletta) have been little studied, even though the habitats they breed in permit relatively easy observation of their behavior and examination of other aspects of their biology. General natural history observations include those of Johnson (1933), Pickwell (1947) and Bent (1950), Sutton and Parmelee (1954) discussed survival problems of Water Pipits in the Arctic, and Verbeek (1970) provided data on the breeding biology of an alpine population, the most comprehensive account to date. Details of the foraging ecology and reproductive biology of European Water Pipits are available in Gibb (1956) for a coastal-breeding population, and in Catzeflis (1978) for an alpine-breeding population.

In this paper I describe how alpine-nesting Water Pipits use space around their nests when foraging for themselves and their nestlings. In particular, I examine (1) whether or not pairs of foraging pipits divide up available food resources and, if so, in what way(s), (2) how foraging behavior changes with increasing age of the nestlings, and (3) in what ways, if any, pipits adjust their foraging behavior to reduce the risk of nest detection by predators. I also test the hypotheses that (1) foraging patterns can be predicted based on measures of relative parental investment, and (2) patterns of foraging are stereotyped, sex-specific behaviors. I compare these results with those available for other bird species to identify common patterns.

STUDY AREA AND METHODS

The study area was located in alpine tundra on the Beartooth Plateau, Park County, Wyoming, just below Beartooth Pass, at about 3200 m elevation. I centered my study site around the large, permanent snowfield at the base of what Verbeek (1970) termed "Pipit Hill." This area encompassed four principal habitat types. The first type I called tundra meadow. This corresponds to Pattie and Verbeek's (1966) dry meadow association and is typified by a ground cover of a variety of forbs and grasses. Maximum vegetation height was about 15 cm. The second type I called fellfield, corresponding to Pattie and Verbeek's (1966) type of the same name. This type supports mostly cushion plants and a few scattered forbs and grasses, but is at least 40-50% bare rock and soil. Most of the vegetation is less than 2 cm tall. The third type I called snowfield, which is essentially a two-dimensional habitat of permanent or semipermanent snow. The fourth type I called "other"; it encompasses rock outcrops, talus, and pond margins. Each of the "other" subtypes was essentially free of vegetation and snow. For additional descriptions of the site, and the Beartooth area in general, see Johnson and Billings (1962), Pattie and Verbeek (1966) and Verbeek (1970).

I located active Water Pipit nests in snow-free areas adjacent to the permanent snowfield of my study site (see Verbeek 1970) during the summers (June-August) of 1983 and 1984. I concentrated my observations of foraging activities on six (focal) nests, each located 20-60 m from the nearest snow at the time eggs hatched.

I captured adult females of each of the six pairs with a butterfly net while they were on their nests, banded them with color and U.S. Fish and Wildlife Service aluminum bands, and marked them additionally with a dab of yellow acryllic paint on the backs of their heads. Adult males were not captured, but I am confident that sex determination was accurate because only female Water Pipits incubate and brood (Verbeek 1970). At each of the six nests only the color-marked bird incubated the clutch and brooded the nestlings.

After eggs hatched in the six focal nests, I recorded where the pipits traveled along the eight principal compass directions when adults departed from the nest on foraging trips. I observed the nests with a 9X binocular from a position at least 60 m from each nest. At this distance the adults appeared undisturbed by my presence so long as I remained relatively inactive. I made observations throughout the daylight hours in two-hour sessions. Distances and directions traveled were recorded in reference to series of stakes placed at 20 m intervals for 40 m along the four cardinal directions around each nest. The farther a bird traveled, the greater became the error of the estimated distance traveled. To minimize this problem I paced distances from each nest to distant landmarks, which I used as reference points when making estimates of the longer foraging trips. I also used distances between my stakes as a scale for foraging trips that were to points nearer the nest. For each trip I recorded time, sex, if a fecal sac was carried in the bill when departing, direction, distance traveled, and habitat visited. For the last three variables I recorded only where foraging was first initiated, because I felt this was most representative of where the bird decided foraging might be most profitable on a new foraging trip, and I could then concentrate my attention on activities at the nest. I made maps of total foraging areas for each pipit by plotting the point of the longest observed trip along each of the eight compass directions, and connecting these points to form a convex polygon around each nest. By weighing cutouts of these polygons and comparing these with the weight of a 1 ha cutout drawn to the same scale as the foraging area maps, I calculated foraging areas for each bird.

I calculated the amount of overlap in the orientation of foraging trips between members of pairs using the Proportional Similarity Index (Feinsinger and Spears 1981)

$$[1] \qquad PS_j = 1 - 0.5\sum|p_{ij} - q_{ij}| = \sum \underline{\min}\,(p_{ij}, q_{ij})$$

where PSj is the overlap in the distribution of foraging trip departures (degree of similarity of departure orientation) at nest j, pij is the proportion of foraging trips in direction i by male j, and qij is the proportion of foraging trips in direction i by female j. Values can range from 0 (no overlap) to 1 (complete overlap).

From study skins I measured five morphological characters pertinent to foraging behavior and the capture of food. To reduce the possible influence of interdemic variation in morphology on my results I measured only adult Water Pipits collected on the Beartooth Plateau. These specimens are currently in the collection of the University of Montana Bird and Mammal Museum, in the

Department of Zoology. The measurements taken are defined as follows: bill length--the distance between the anterior margin of the nostril and tip of the upper mandible; bill depth--the distance (chord) from the culmen to the lower edge of the ramus of the mandible at the anterior margin of the nostril; bill width--the distance (chord) between the tomium of the upper mandible at the anterior margin of the nostril; tarsus length--the distance from the point of the joint between the tibia and metatarsus to the point of the joint at the base of the anterior surface of the front middle toe; wing length--the chord of the unflattened wing when closed.

All statistical procedures used are described in Sokal and Rohlf (1981); all significance levels were set at $\alpha = 0.05$.

RESULTS

MORPHOLOGICAL CHARACTERS

No significant differences between the sexes were detected for four (bill length, bill depth, bill width, tarsus length) of the five characters (t-tests, Table 1). Only the difference in wing length was significant ($t = 9.049$, $df = 31$, $P < 0.001$), with adult males having longer wings.

INTRAPAIR DIFFERENCES IN HABITAT USE

There were no consistent differences in habitat use between members of pairs. Three of the pairs showed significant differences between the sexes (pairs 1, 2, and 9)(Table 2) while the other three (pairs 7, 15, and 16) did not, though pair 16 approached significance ($G = 7.199$, $df = 3$, $0.1 > P > 0.05$). Males tended to visit tundra meadow and snowfield sites on a greater proportion of their foraging trips than did females, while females tended to visit fellfield and "other" sites more often than did males. However, in some cases the sample sizes are very small, while in other cases the differences in proportions are minor. The trends may actually be nothing other than sampling artifacts. Nearly all members of pairs used either tundra meadow or fellfield sites significantly more often than expected (10 of 12 cases) and snowfield sites significantly less than expected (11 of 12 cases), based on habitat availability (Hendricks, unpublished manuscript). This indicates that the way the sexes respond to a heterogeneous environment is similar in manner but different, in some cases, in magnitude.

Table 1. Average measurements of the morphological characters (mm ± SD) of adult water pipits from the Beartooth Plateau, Wyoming. Numbers in parentheses are sample sizes.

Morphological Character	Males	Females	t	P
bill length	9.36 ± .32 (17)	9.21 ± .19 (9)	1.875	>0.05
bill depth	3.33 ± .15 (16)	3.36 ± .13 (9)	0.50	>0.5
bill width	3.31 ± .14 (15)	3.34 ± .14 (8)	0.492	>0.5
tarsus length	21.79 ± .53 (18)	21.46 ± 1.03 (9)	1.107	>0.2
wing length	87.3 ± 2.5 (21)	81.3 ± 1.7 (12)	9.049	<0.001

Table 2. Number of visits to each of the habitats by members of pairs of water pipits (males, females).

Pair	Tundra Meadow	Fellfield	Snowfield	"Other"	G^a
1	110, 222	13, 91	3, 0	10, 0	46.385**
2	312, 236	51, 17	23, 5	14, 17	17.663**
7	68, 38	5, 4	1, 2	0, 0	1.245
9	43, 17	18, 21	17, 4	1, 2	10.015*
15	68, 91	5, 8	0, 1	1, 9	5.017
16	88, 32	12, 14	1, 0	1, 2	7.199

[a] RXC test of independence, William's correction, df = 3

*$P < 0.025$, **$P < 0.001$

DISTANCES TRAVELED

Water Pipits foraged frequently beyond the areas they actively defended (roughly 40 X 40 m) around their nests, and intrusion on other pipit territories was common. However, there appeared to be large areas of undefended terrain on my study site. This permitted pipits to forage large distances from their territories (sometimes greater than 300 m) without being attacked by other pipits. Total foraging areas used by the six focal pairs ranged from 3.29 to 10.14 ha ($\bar{X} = 6.73 \pm 2.43$ SD). For males these areas ranged from 1.76 to 10.14 ha ($\bar{X} = 5.25 \pm 2.80$ SD), while foraging areas for females ranged from 2.21 to 6.63 ha ($\bar{X} = 3.64 \pm 1.57$ SD). Mean foraging areas of the sexes did not differ significantly ($t = 1.227$, $df = 10$, $P > 0.2$).

No specific trend was detected in sex differences in mean distances traveled by each pair of pipits (Table 3). The means of four of six pairs are significantly different. Of these, males had longer mean distances in three of four cases (pairs 1, 2, and 9), and females in the other case (pair 15). In the two cases in which the differences were not significant (pairs 7 and 16) the females traveled slightly longer mean distances. The extreme mean distance traveled by male 1 reflects his attendence at two nests concurrently, located approximately 120 m apart. A large proportion of his departures from nest 1 were oriented towards the general area of the second nest.

Mean distances traveled can be misleading concerning how members of pairs use space around a nest, if the values obtained are from all foraging trips combined. Greater overall mean distances

Table 3. Distances (m) from the nest that male and female water pipits flew to forage during the nestling period.

	Males		Females		
Pair	No. Trips	$\bar{X} \pm SE$	No. Trips	$\bar{X} \pm SE$	P[a]
1	136	174.6 ± 6.4	313	40.1 ± 1.9	<0.001
2	400	68.8 ± 3.1	275	38.1 ± 1.3	<0.001
7	74	86.6 ± 4.8	44	90.5 ± 8.5	NS
9	79	88.7 ± 5.7	44	62.7 ± 4.3	<0.01
15	74	40.9 ± 4.4	109	56.1 ± 3.4	<0.001
16	102	86.3 ± 5.0	48	89.3 ± 7.8	NS

[a] Mann-Whitney U test

traveled could result from long trips taken on only one or two directions from the nest. To see if this was the case for the Water Pipits, I examined the relationship between mean foraging distance and direction traveled for each sex at each of the nests (Figure 1). There was no significant trend apparent (goodness-of-fit test, $G = 3.643$, $df = 1$, $0.1 > P > 0.05$) in which sex traveled farthest from the nest, although the difference approached significance. This result was probably greatly influenced by activities at nests 1 and 2, where males had the greatest mean distances traveled on seven of eight and eight of eight directions, respectively.

Trips on which fecal sacs were carried were consistently farther from the nest than were trips without fecal sacs, for all pairs with mates combined (Mann-Whitney U test; $P < 0.05$ for nest 1, $P < 0.01$ for nest 16, $P < 0.001$ for nests 2, 7, 9, and 15). The relationship is the same for individuals of pairs as well (Table 4). All individuals except males 1 and 16 traveled significantly farther from nests when departing with fecal sacs. Male 1 tended two nests and concentrated the majority of his trip departures toward the second nest, usually flying most of the distance to the second nest before landing. He usually departed in that direction whether or not he carried a fecal sac. The relationship for male 16 is less easy to explain, though it should be noted that the difference in distance traveled approached significance ($P = 0.086$). On 26 July 1984 the contents of nest 16 were nearly discovered by a long-tailed weasel (Mustela frenata), the only one of my study nests where I saw this occur. Both adults acted as though they were alarmed and remained so for several hours. This incident may have induced male

Figure 1. Comparison of male and female foraging distances for six pairs of Water Pipits. Each point represents the mean distance flown in one direction by a male plotted against that flown by his mate. The number of directions plotted for each pair is eight. The diagonal line indicates where distances flown by mates are equal.

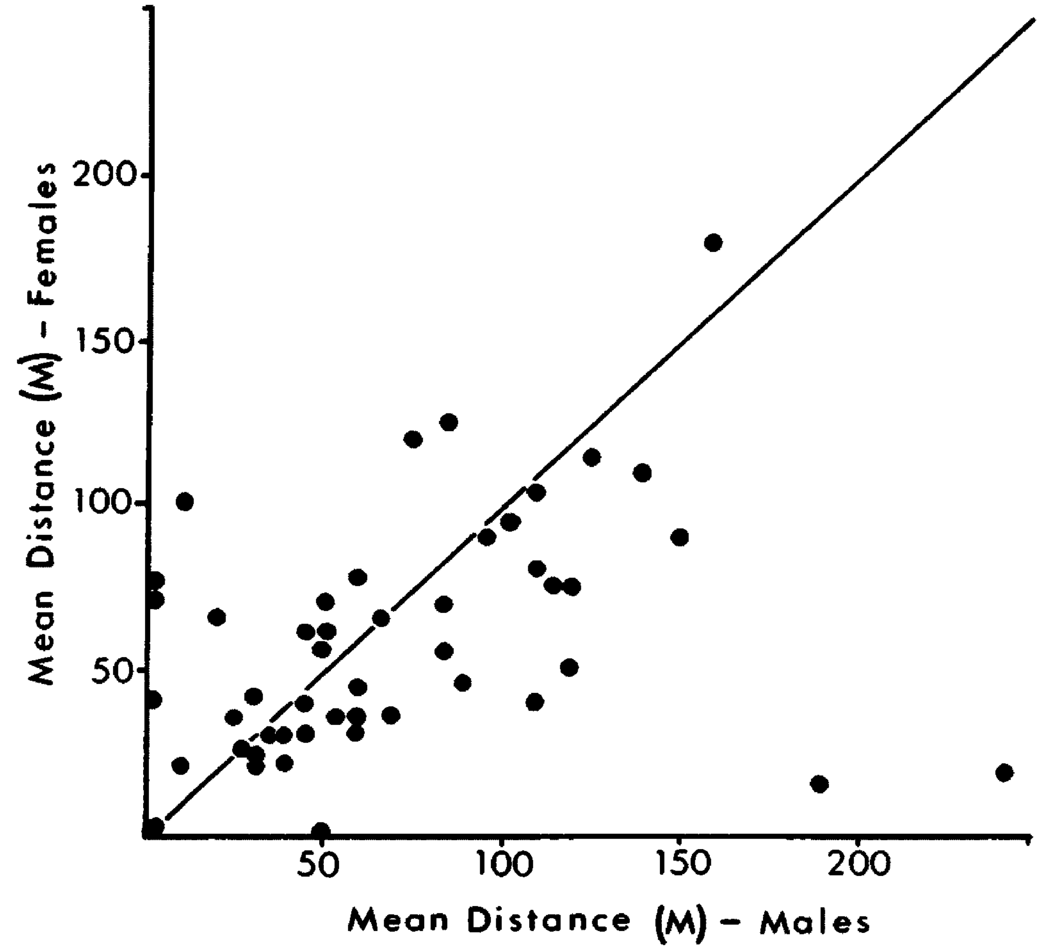

Mean Distance (M) - Females
200
150
100
50
50
100
150
200
Mean Distance (M) - Males

Table 4. Distances (m) from the nest that pairs of water pipits flew to forage ($\overline{X}$ ± SE), when departing with and without fecal sacs.

Nest	without fecal sac	(n)	with fecal sac	(n)	P[a]
1					
male	172.3 ± 6.8	115	187.1 ± 18.1	21	>0.5
female	36.1 ± 2.2	238	53.1 ± 3.0	75	<0.001
2					
male	61.8 ± 3.3	331	102.2 ± 7.9	69	<0.001
female	34.9 ± 1.3	211	48.4 ± 3.4	64	<0.001
7					
male	78.2 ± 5.5	59	119.3 ± 4.4	15	<0.001
female	70.0 ± 7.1	30	134.3 ± 16.9	14	<0.001
9					
male	74.0 ± 4.4	67	171.7 ± 10.8	12	<0.001
female	48.5 ± 4.2	27	85.3 ± 5.6	17	<0.001
15					
male	33.0 ± 5.9	50	57.5 ± 4.8	24	<0.001
female	40.9 ± 3.4	68	81.2 ± 4.9	41	<0.001
16					
male	84.1 ± 5.7	87	98.6 ± 8.8	15	<0.1
female	80.2 ± 7.8	42	153.3 ± 11.1	6	<0.001

[a] Mann-Whitney U test

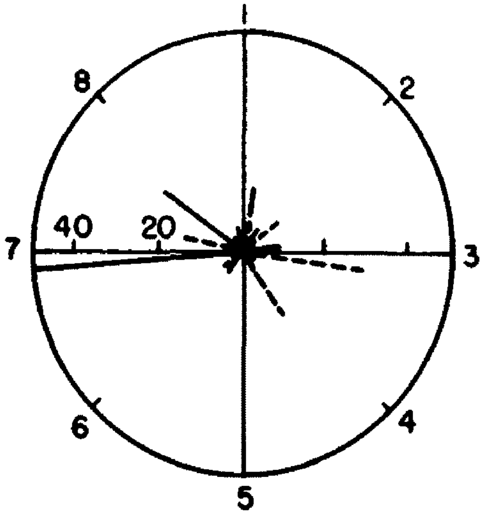
16 to remain closer to the nest than he had previously (the female brooded part of this time), in order to monitor the nest more easily.

The pattern of traveling greater distances with fecal sacs was particularly striking for some trips. On several occasions pipits departed from the nest in one direction with a fecal sac, dropped the sac while in flight (or sometimes even landing first), then changed directions (as much as 90°) and continued elsewhere to begin foraging. For trips like this I recorded only straight-line distances from the nest to where foraging began. Thus, the variance in distances traveled and the magnitude of the differences presented in Table 4 are not entirely representative of the extra effort adults were making to dispose of fecal sacs.

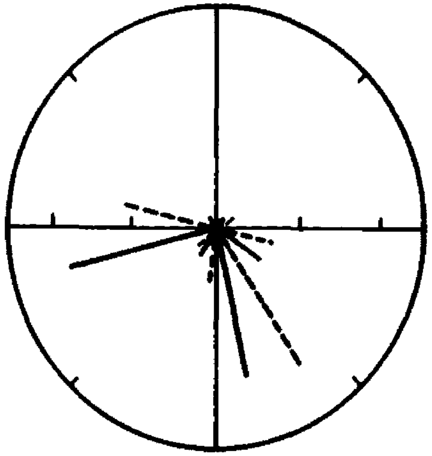
ORIENTATION OF DEPARTURES FROM THE NEST

Water Pipits tended to forage alone, and the individuals of a pair foraged in significantly nonoverlapping directions from the nest (R X C test of independence)(Figure 2). Even when members of a pair were at the nest together, they usually departed in different directions. The Proportional Similarity Indices calculated from [1] for pairs 1, 2, 7, 9, 15, and 16, respectively, were 0.437, 0.621, 0.668, 0.393, 0.523, and 0.696. These numbers can be interpreted to mean that, between mates, 30-60% of the total departures from nests were in different directions. For all individuals, with the exceptions of females 15 and 16, the direction of departure was significantly nonrandom (Rayleigh test, Batschelet 1965)(see Figure 2). Taken together, these results indicate that members of pairs

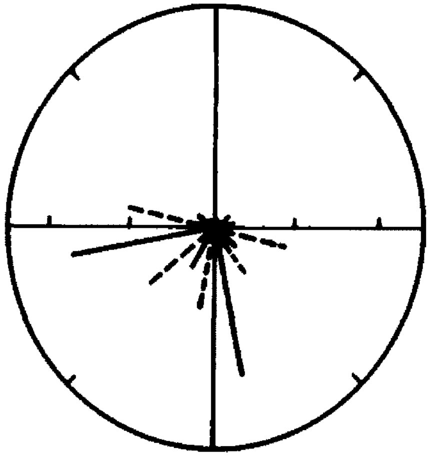
Figure 2. Directions from the nest (in percentage of total trips for each bird) in which male and female Water Pipits flew to forage during the nestling period. Intervals of 20% are marked on the horizontal axis of each circle. Males are solid lines, females are dashed lines. Total observations for each bird are given below the respective circle. P values are significance levels, based on a R X C test of independence (with William's correction; df = 7), comparing the distributions of trips by members of a pair. All individuals show significant, nonrandom, degrees of concentration of foraging trips (Rayleigh test, $P < 0.01$) (Batschelet 1965) except females 15 ($r = 0.051$, $P > 0.05$) and 16 ($r = 0.145$, $P > 0.05$).



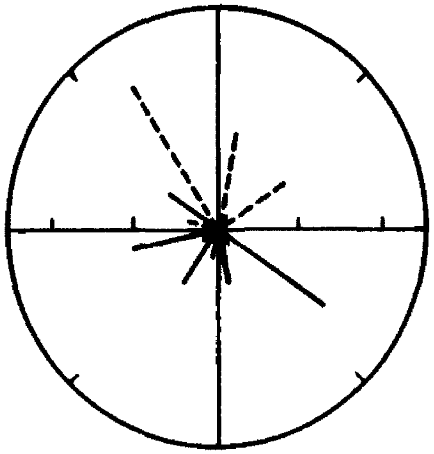
NEST 1
$P < 0.001$
OBS. MALE 136
OBS. FEMALE 313



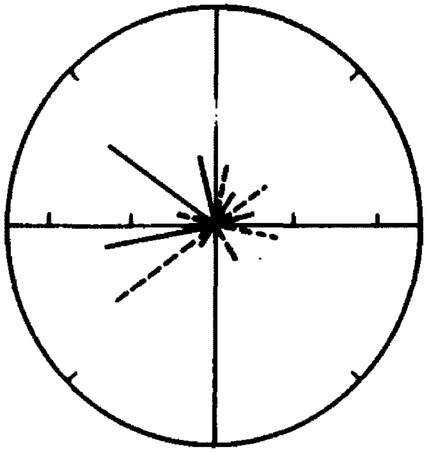
NEST 2
$P < 0.001$
OBS. MALE 400
OBS. FEMALE 275



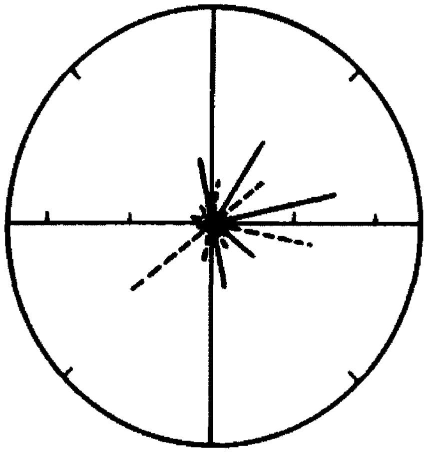
NEST 7
$P < 0.05$
OBS. MALE 74
OBS. FEMALE 44



NEST 9
$P < 0.001$
OBS. MALE 79
OBS. FEMALE 44



NEST 15
$P < 0.001$
OBS. MALE 74
OBS. FEMALE 109



NEST 16
$P < 0.001$
OBS. MALE 102
OBS. FEMALE 48

tended to forage apart.

DELIVERY RATES AND NESTLING AGE

Female pipits brooded the nestlings for a large proportion of the day during the first few days after hatching. Diurnal brooding ceased about the fifth day after hatching. During these first few days of nestling life the male delivered most of the food to the nestlings. Later, deliveries are roughly equal for males and females (Verbeek 1970, pers. obs.). As nestlings grew older, delivery rates of food to the nests increased significantly (Figure 3). Also, as the delivery rates increased, foraging trips became significantly shorter (Figure 4). Thus, as the nestlings grew older and increased their demands for food, the adults tended to concentrate their foraging closer to the nests.

PARENTAL INVESTMENT

During the nestling phase at four of six nests, male pipits made more food deliveries than did females (Table 3). At each of the six nests the difference in the number of deliveries by each sex was significant (Chi-squared tests; $P < 0.01$, $df = 1$). At five of six nests females carried fecal sacs on a greater percentage of nest departures than did the respective males. Overall, females carried fecal sacs on 28.0% (± 9.1 SD) of nest departures (217 of 833 trips), whereas males carried fecal sacs on 19.2% (± 6.2 SD) of nest departures (156 of 865 trips)(extracted from Table 4). The pooled data show that the tendency to carry fecal sacs was not independent of parental sex (test of independence with Williams' correction; G =

Figure 3. Comparison of the rate of food deliveries to nests in relation to the age of nestling Water Pipits. Each point represents one day's observation for one pair.

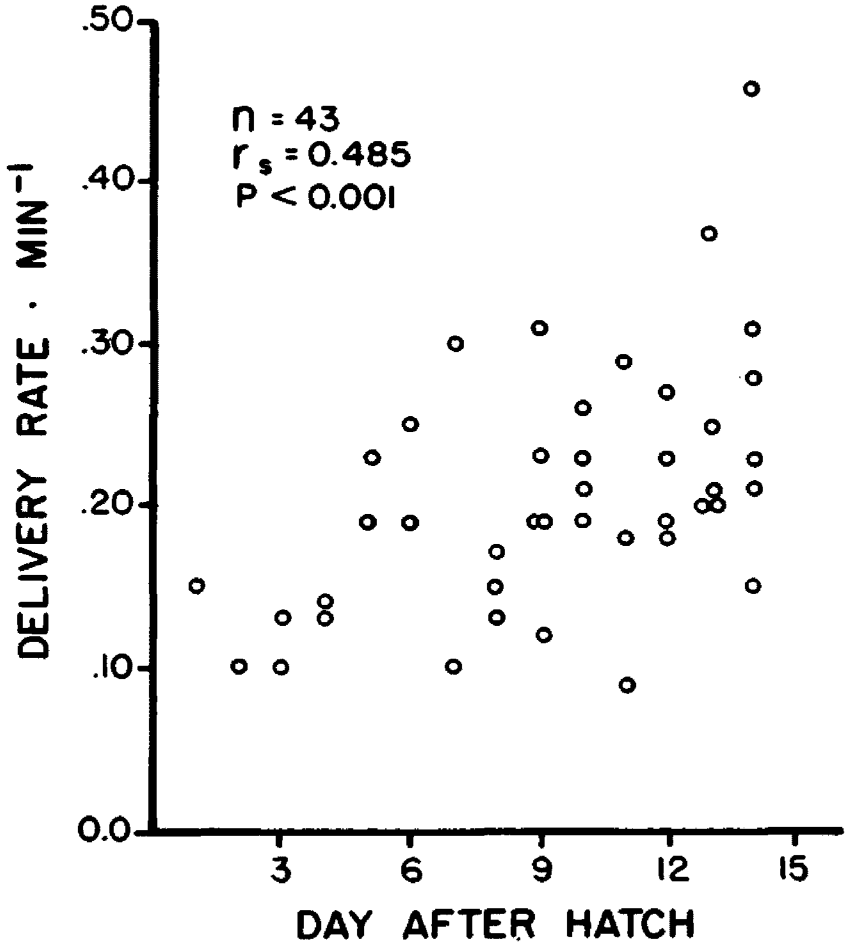
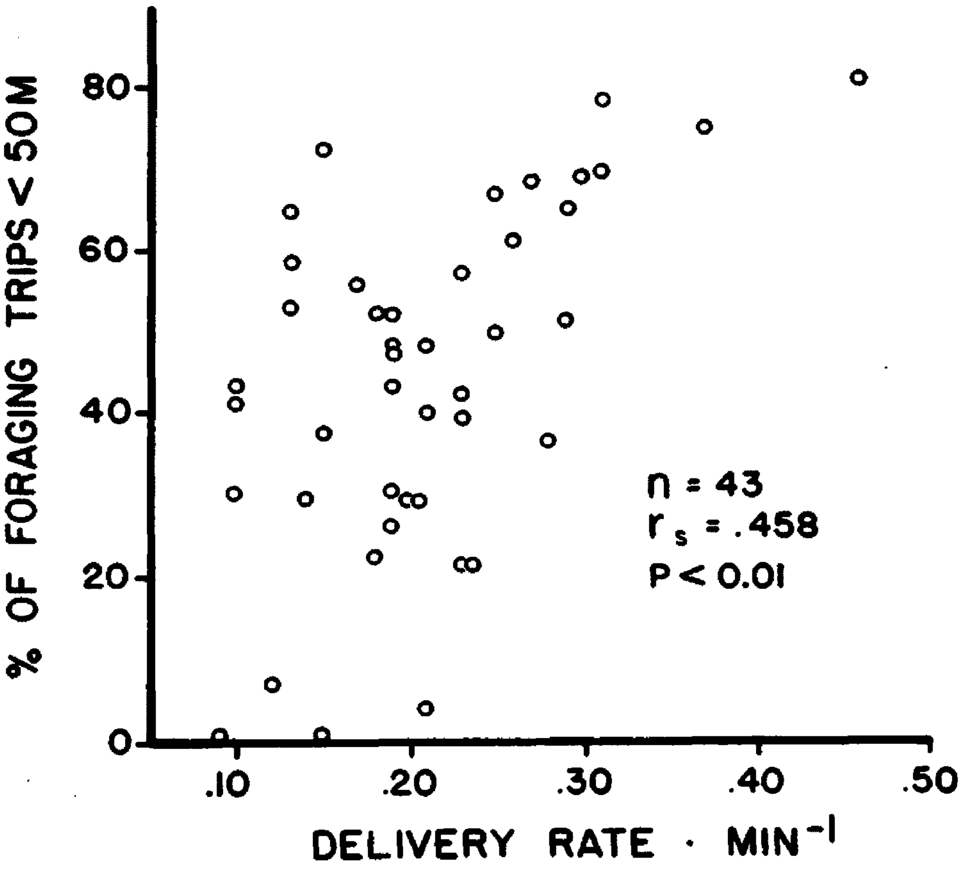

n = 43
r_s = 0.485
P < 0.001
.50
.40
.30
.20
.10
0.0
DELIVERY RATE · MIN^{-1}
3
6
9
12
15
DAY AFTER HATCH

Figure 4. Comparison of the percent of foraging trips < 50 m from nests in relation to the rate of food deliveries to nests. Each point represents one day's observation for one pair.


% OF FORAGING TRIPS < 50M
80
60
40
20
0
.10
.20
.30
.40
.50
DELIVERY RATE · MIN⁻¹
n = 43
r_s = .458
P < 0.01

15.94, df = 1, $P < 0.001$). At all nests only females incubated and brooded. As mentioned previously, brooding continued until the fifth day after hatching (Verbeek 1970, pers. obs.).

DISCUSSION

DIFFERENTIAL NICHE UTILIZATION

Charnov et al. (1976) listed three ways by which coexisting predators may divide food resources if resource depression is a possible result of living in proximity to each other. Although their discussion concerned different kinds of predators, the three ways they presented, plus an additional method I include here, may also apply to pairs of nesting birds engaged in biparental care.

First, food resources may be divided by hunting for different subsets of the available food. For species where the sexes are dimorphic in feeding structures, such as some Hawaiian honeycreepers and some woodpeckers (Selander 1966, 1972; Martindale 1983), these differences are related to the exploitation of different sources of food. In general, a knowledge of feeding behavior and bill morphology is sufficient to determine the important aspects of foraging ecology of insectivorous birds (Cody 1974, Robinson and Holmes 1982). Water Pipits are monomorphic (Verner and Willson 1969) in most respects, including the structures associated with foraging (Table 1). Only wing length differed between the sexes. This difference could have evolved in response to selection for more efficient flight by males (e.g. Feinsinger and Chaplin 1975), perhaps in association with the extensive aerial song displays that males use when establishing territories (Verbeek 1970, pers. obs.). Since bill characters of male and female pipits are the same, and since the sexes forage in the same habitats, it is reasonable to conclude that they capture the same types of prey. This is supported by my observation that the larger prey types (caterpillars, spiders, and grasshoppers) were delivered in equal proportions to the nests by both sexes (no. deliveries: males = 36, females = 39). Both Robins (1971) and Knapton (1980) found no differences in the kinds of prey delivered to nestlings by male and female Henslow's Sparrows (*Ammodramus henslowii*) and Clay-colored Sparrows (*Spizella pallida*), respectively. The latter two species are sexually monomorphic and occupy habitats of short vertical dimensions somewhat like alpine tundra.

Second, food resources may be partitioned by using different foraging behaviors, such that the birds encounter and capture the kinds of prey that they do as a result of the way that they hunt. Power (1980) found this to be the case for Mountain Bluebirds (*Sialia currucoides*), where there were no overall differences between sexes in the types of prey delivered to nests, but females tended to forage more by hovering and hawking than did males. The opportunities to divide food resources through behavioral differences in foraging are restricted in an environment of simple structure. Water Pipits foraged almost exclusively by walking or running briefly, and picking arthropods off of vegetation and the ground by gleaning and pecking. There were no discernable sex differences. Robins (1971) also reported similarities in foraging behavior for pairs of Henslow's Sparrows.

Third, food resources may be divided between the sexes by foraging at different times of the day. Knapton (1984a) found evidence of this pattern in Nashville Warblers (*Vermivora ruficapilla*), where females made significantly more feeding trips to the nest in the mornings and evenings than did the males. I noticed no such trend in Water Pipits, though I did not design my field work to address this possibility. For three pairs, males consistently made more foraging trips on the days sampled than did the females, the reverse was true for two pairs, while for the sixth pair the male started by making more trips, then the female did so, and by the time of fledging the adults were making an equal number of trips. Whether such individual consistency in day-to-day results also applies on an hour-to-hour basis will have to await future research.

Fourth, sexes may divide food resources by foraging in different places. Space can be divided in different ways, depending on the structure of the habitat. In complex habitats with large vertical components, such as forests, there can be sexual differences in the foraging heights, foraging substrates (trunks, branches, etc.), or tree species. Each of these methods of partitioning has been documented; woodpeckers (Selander 1966, 1972), vireos (Williamson 1971, Holmes 1986), warblers (Morse 1968, Holmes et al. 1978, Franzreb 1983), tanagers and grosbeaks (Holmes 1986) use the first method, other woodpeckers (see Selander 1966, 1972) the second method, and still other woodpeckers (Martindale 1983), vireos (Holmes 1986), warblers (Franzreb 1983, Holmes 1986), and grosbeaks (Holmes 1986) the third method. Bird species that are monomorphic, and that occupy a simple two-dimensional habitat, face a different situation. They are unable to partition space vertically. This led Robins (1971) to hypothesize that monomorphic species in simple habitats would show spatial partitioning, with pairs foraging at different horizontal distances from the nest. He further hypothesized that the individual making the largest energy investment in the offspring should have preferential access to areas closest to the nest, thereby reducing energy expended while foraging. Female Henslow's Sparrows forage closer to the nest than do males, and mates tend to forage in different places (Robins 1971). Female White-throated Sparrows (Zonotrichia albicollis) forage closer to nests (Wasserman 1986), and Clay-colored Sparrows also show the same pattern (Knapton 1980). In contrast, Brooke (1981) detected no sex differences in the distances foraged from the nest by pairs of Wheatears (Oenanthe oenanthe). For Water Pipits, where it is not clear which parent is making the larger energy (parental) investment in the offspring, the pattern is similar in some ways to both Wheatears and the two sparrow species. There were no consistent trends with regard to which sex foraged farthest from the nest (Table 3, Figure 1), although the differences were significant in four of six cases. All pairs did show significant differences in foraging areas (directions), however (Figure 2). Use of different foraging areas has also been documented for Meadow Pipits (A. pratensis) (Seel and Walton 1979) and Lapland Longspurs (Calcarius lapponicus) (Tyron and MacLean 1980).

It is worth noting that the Water Pipits divided space in a different manner at each nesting attempt (Table 2 and 3, Figure 2). Such variability has been reported by Robins (1971) and Holmes et al. (1978) for other species. This indicates not only that there are problems with predicting behavioral or ecological patterns based on parental investment alone (see Knapton 1984b), but that the manner of differential niche utilization cannot be attributed entirely to sex-specific stereotyped behavior (Robins 1971), as has been suggested by Jackson (1970) to be the case for woodpeckers. Thus, the hypotheses that (1) patterns of foraging may be predicted on the basis of parental investment (an energetics argument), and (2) foraging patterns are stereotyped and sex-specific are not supported by the data presented in this paper. These and other data suggest that a complex interaction of social and environmental variables are at play, and that there is a need for more refined analysis before the behavior of many species can be accurately predicted.

The proximate mechanisms maintaining the division of space are not known, but it is possible that the sexes learn to avoid localities where their mates prefer to forage, because it is less profitable to forage there themselves. It is also possible that females dominate males during the breeding season, and forage in areas they prefer, with males trying to avoid these sites. Such has been hypothesized by Kamil and van Riper (1982) for the Amakihi (*Loxops virens*), and has been suggested as the pattern of dominance for monogamous bird species in general (Smith 1980). On two occasions I saw male Water Pipits land near where their mates were foraging, shortly to be chased away by the females. The reverse was never seen. In fact, I almost never saw a known mated pair of pipits together anywhere other than at the nest. This supports Smith's (1980) hypothesis, although my sample size is too small to generalize reliably.

FORAGING PATTERNS AND PREDATOR AVOIDANCE

Models of foraging behavior, particularly optimal foraging theory (Pyke et al. 1977), have been very useful in predicting how organisms should go about acquiring food. However, only recently have researchers begun to measure the influence of predation in shaping behaviors (for example Caraco et al. 1980, Sih 1980). Predation on nests is an important element in the breeding ecology of Water Pipits (Verbeek 1970). In the 16 nests located during my study, two females were killed on their nests, one clutch was destroyed, and two broods were depredated, for a loss of 31.3% of the nests to predators. Measuring how predation may influence behavior is difficult, but two lines of evidence suggest that predator avoidance can significantly influence how Water Pipits go about acquiring food for their offspring.

An increase in the number of food deliveries to nestlings as they age has been reported elsewhere (see Johnson and Best 1982), and occurs in Water Pipits as well (Figure 3). Also, as the rate of deliveries to the nest increased, the pipits foraged closer to their nests (Figure 4). Brooke (1981) found the same pattern for nesting Wheatears, and speculated that it was an adaptation to elude predators. He suggested that adults foraged farther from the nest than was optimal early on to reduce the probability of nest detection, because he found that food was equally abundant throughout the habitat around the nests. A Wheatear trying to maximize energy intake, without being concerned with predation, should have used the resources closer to the nest. Distributions of prey organisms at the Beartooth study site (Hendricks, unpublished manuscript) lead me to suggest that a similar situation exists for Water Pipits in alpine habitats. Elsewhere, Martindale (1982) found that Gila Woodpeckers (Melanerpes uropygialis) responded to intruders (or potential predators) near the nest by foraging closer to the nest following intrusions. This permitted the adults to forage and monitor the nests at the same time. The greater the length of time between intrusions, the more time adults spent foraging at greater distances from the nests. These results indicate that distance foraged from the nest is a compromise between demands for maximizing the acquisition of energy and minimizing the risk of nest loss.

A second line of evidence suggesting that predation influences foraging patterns is provided by how adult birds dispose of fecal sacs. Foraging trips on which pipits carried fecal sacs were significantly farther than trips without sacs (Table 4). Brooke (1981) found the same pattern for nesting Wheatears. The assumption here is that the presence of fecal sacs at or near a nest increases the probability that a predator will locate the nest, in much the same way as might occur from the presence of egg shells (Tinbergen et al. 1963). Conclusive evidence for this hypothesis is lacking, but it is certain that disposal of fecal sacs requires some sort of cost to the bird disposing of the sac (Weatherhead 1984) and the greater the distance the sac is carried the greater the cost. Nest sanitation and predation are two hypotheses used to explain the removal of fecal sacs. It is unlikely, however, that nest sanitation can explain why birds carry feces up to 100 m from the nest, as Water Pipits will do. The predation avoidance hypothesis is the most parsimonious of the two.

I suggest that predation may influence fecal sac removal from Water Pipit nests in two ways. First, fecal sacs are removed from the close vicinity of the nest in response to predation pressure from mammals, such as weasels and foxes, and birds, such as Common Ravens (Corvus corax), all of which were seen several times on my study site. Second, fecal sacs are carried distances greater than necessary to deter ground predators, in response to predation pressure from keen-visioned aerial predators (ravens). If a pipit carries fecal sacs long distances, it is less likely to reveal the location of the nest, since the area the predator needs to search to locate the nest is too great to make the search profitable. Due to the better visual acuity and perspective of the aerial predator, coupled with the open nature of the alpine environment, pipits have to carry fecal sacs the extra distance to minimize nest detection. Field experiments to test these hypotheses should be feasible.

Antipredator defenses during reproduction are important components in determining how much energy can be allocated for parental care. The more energetically costly the defensive processes are, the greater will be the impact on avian reproductive strategies, through changes in clutch size, length of the nestling period, the selection of nest sites, and so on (Ricklefs 1977). Future studies of parental investment and foraging behavior of breeding birds should include analyses of the potential influence of predator avoidance in structuring the patterns of foraging (Holmes 1986) and reproduction observed.

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