

## BREEDING ECOLOGY OF THE WATER PIPIT

NICOLAAS A. M. VERBEEK

THE Water Pipit (*Anthus spinoletta*) is a holarctic bird breeding in alpine and arctic habitats. Probably because of its remote distribution, little information on the species is available. In North America, Johnson (1933) reports observations on one nest of *A. s. rubescens* in Labrador. Pickwell (1947) gives details on adult behavior and on three nests of what was probably *A. s. pacificus* on Mt. Rainier, Washington. Sutton and Parmelee (1954) give data on 14 nests and discuss survival problems on Baffin Island. Irving (1960a) discusses nutritional conditions of pipits arriving on their Alaska breeding grounds. Drury (1961) reports on one nest from Bylot Island, Northwest Territories and discusses ecological relationships between the pipit, Horned Lark (*Eremophila alpestris*), Lapland Longspur (*Calcarius lapponicus*), and Snow Bunting (*Plectrophenax nivalis*). In Europe, Gibb (1956) studied food and ecology of *A. s. petrosus* along the coast of Cornwall, England, and Ringleben (1957) deals with migration and habitat preference of *A. s. spinoletta* in Lower Saxony, Germany.

This paper deals with *A. s. alticola*. The study was conducted from 14 June to 21 September 1963 and from 12 June to 20 August 1964. The objectives were to obtain details on the species' breeding biology and its adaptations to breeding in the alpine environment.

### STUDY AREA

The main study area (Figure 1) was about 116 hectares of alpine tundra on the Beartooth Plateau, Wyoming, circa 45° N and 109° 30' W. The average altitude is 3,200 m, with a range of about 140 m.

Bamberg (1961) and Johnson and Billings (1962) describe the vegetation; Nimlos and McConnell (1962) the soils; Nimlos et al. (1965) the soil temperature and moisture conditions. For a description of the vegetation relevant to this study see Pattie and Verbeek (1966).

The alpine climate typically has cool air temperatures, intense radiation, great diurnal temperature extremes, strong winds, and snow almost any month of the year. Table 1 shows climatic data for the 1963 and 1964 seasons. Because pipits spend most of the time on the ground, I measured ground level temperatures at 5 cm above ground at one station in the valley and one on Pipit Hill in 1964.

The 1963 breeding season was much wetter with more snow, hail, and sleet than the 1964 season. Snow falling in July and August usually stays on the ground only for the duration of the storm or for a short time thereafter. Thundershowers, accompanied by hail and occasional sleet, are

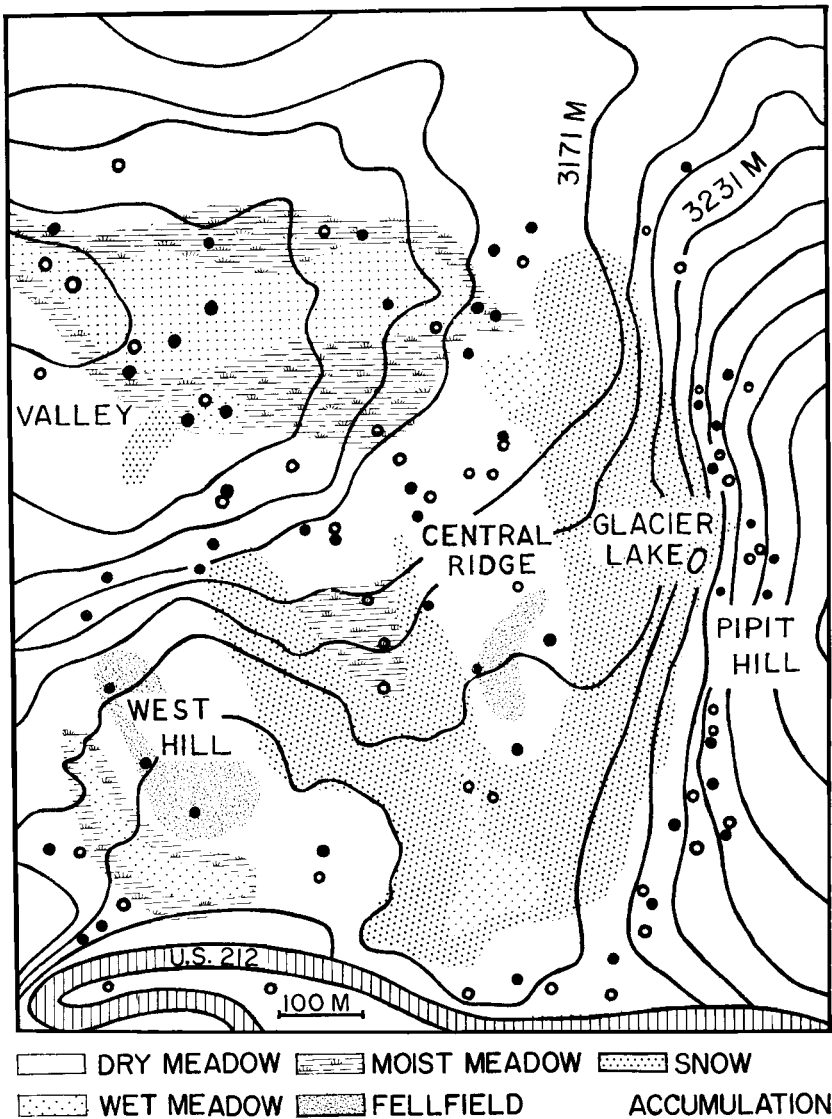


Figure 1. Topography of the study area and distribution of nests of the Water Pipit in 1963 (circles) and 1964 (dots). Contour interval is 30 m.

common throughout the season. Depth of snow deposited during the winter varies with the degree of exposure and is modified by "the prevailing winds during and immediately following the winter snow storms" (Johnson and

TABLE 1  
MEAN TEMPERATURE AND TOTAL PRECIPITATION ON THE STUDY AREA

Period	Max. temperature (°C)		Min. temperature (°C)			Precipitation (mm)				
	Standard shelter		Standard shelter			Rain		Snow		
	1963	1964	1964	1963	1964	1964	1963	1964	1963	1964
15-30 June	11.0	8.8		-1.4	0.2		11.2	21.6	9.7	7.8
1-31 July	15.3	17.0	30.8	3.2	3.9	1.1	54.1	23.7	5.1	0.0
1-31 Aug.	15.1	12.7	27.2	1.7	0.2	-2.2	12.9	18.3	3.1	220.6
1-20 Sept.	11.2			0.6			63.7		6.6	

Billings, 1962). In 1963 higher temperatures in late June removed the snow much more rapidly than in 1964.

#### SPRING ARRIVAL

Pipits of both sexes were present on the study area when I arrived both years. The road crews told me that pipits are already on the plateau when the pass is opened for traffic the last week of May. Wide variations in their numbers suggest that in the prenesting period pipits move from the alpine meadows to lower altitudes whenever the weather becomes severe, and return as soon as conditions improve. Presence of several single males during this period indicates that at least some males arrive on the breeding grounds unmated.

#### HABITAT AND NEST SITE SELECTION

As the birds arrive before all the snow has left, the first birds occupy snow-free areas as and whenever they appear. More suitable habitat was available earlier in 1963, and nests were found then in places that were either too wet or still snow-covered on the same date in 1964. The location of each nest was determined with the aid of a transit (Figure 1) with reference to known bench marks and plotted. In general the nests were confined to the face of Pipit Hill, the Central Ridge, the north and west faces of West Hill, and scattered throughout the valley. Within these four general areas, especially on Pipit Hill, the birds apparently selected nodes of territories each year, which left much seemingly suitable nesting territory unoccupied.

In 1963 I banded 102 pipits, including 9 adult females. One of these adult females returned in 1964 and nested about 400 m from her previous site. Four banded juveniles also returned. Two nests in 1964 were built on top of nests of the previous year, and at least three nests were built on top of nests built prior to 1963.

Territories occupied a great variety of terrain from fellfield to wet meadow, on level to steeply sloping ground, and bare to well-vegetated surface. Two habitat requirements are apparent: 1) the site must become snow-free early enough in the season, and 2) it must have some rough features such as tussocks, tilted rocks, or eroded spots for nest sites.

Soper (1946), Wynne-Edwards (1952), and Sutton and Parmelee (1954) all state that the Water Pipit prefers mossy slopes with southern exposure. In the Riesen Mountains of Czechoslovakia, Hanzák (1958) found *A. s. spinoletta* is dependent on the presence of rocky slopes and boulder fields and shows no preference for wet areas. This applies also to the Beartooth Plateau.

#### TERRITORY

In 1963 most territories were already established when I arrived. In 1964 before continuous good weather set in, pipits abandoned their territories frequently. Those birds that stayed during snowy periods showed little territorial activity except for an occasional chase. Sometimes birds flushed from what appeared to be their territory and flew away for half a kilometer or more. Throughout these first unfavorable 10 days in 1964, the flight song could be heard. Once the weather changed for the better, territories were set up rapidly and much chasing occurred.

In 1963 I marked and measured the territorial boundaries of five pairs. They varied in extent from 1,580 to 3,355 square meters and averaged 1,810 square meters or roughly an area of 40 by 45 m. These figures show large parts of the study area unoccupied. Many suitable nest sites became snow-free too late in the season, after most birds had established territories. Also about one-sixth of the 116 hectares consisted of unsuitable nesting terrain, such as permanent snow fields and water surfaces. Drury (1961) on Bylot Island, Northwest Territories, gives territorial sizes of "about 100 yards and 200 feet high," or approximately 5,600 square meters, or roughly three times as large as those on the Beartooth Plateau.

The number of known nests in 1963 was 47, and in two known territories I did not locate the nests. In 1964 I found 52 nests. The estimated total for each year was 60 nests, or a population density of 0.5 pair per hectare.

#### DISPLAYS OF THE MALE

*Threat display.*—Males often approach each other almost casually while feeding, with their wings drooped and their tails bobbing. In this and other male displays the wings do not vibrate. The approach is not direct. The birds feed back and forth until they are close to each other, and one then flies at the other. The attacker may pursue the other bird for some dis-

tance, often beyond the attacker's territorial limits. Upon returning the territorial male often settles on an object higher than the surrounding terrain, such as a boulder or a tussock, where he may preen himself, but usually just sits and looks around alertly.

*Alert display.*—The male stands with his tail elevated but not bobbing and his wings drooped. He often assumes this posture on return to his territory from a chase, and also when another pipit flies over his territory. When the display is directed to another pipit flying overhead, it is accompanied by a "pititititi" call.

*Flight display.*—In this display the male rises at an angle about 40 m into the air and then descends to the ground again singing "tjwee, tjwee" continuously. During the descent he raises and spreads his tail widely and extends his wings fully, so that the innermost (ninth) secondary is free from the body. In the descent the phrases of the song follow each other more rapidly than during the rise. Often the bird continues singing for a few seconds after reaching the ground, and occasionally he sings on the ground without a flight display.

Throughout the early phase of the breeding cycle when territorial behavior is strongest, i.e. from the establishment of the territory until part-way through incubation, males often walk about with drooped wings and elevated tail. The tail may or may not bob. This display is a mixture of the first two described above. As the female does not behave in this manner, it helps to distinguish the sexes in the field.

#### NESTS

Nests are built on the ground and are more or less overhung by rock, sod, or vegetation (Pickwell, 1947; Sutton and Parmelee, 1954; Drury, 1961). The 99 nests I located were of four types. Sod nests (32) are placed at the foot of a tussock or inside clumps of vegetation. Erosion nests (22) are in places where the turf has been broken by erosion; some nests in this category are more exposed than any other type because of the absence of vegetation. Rock nests (28) are situated under the edge of a rock and usually are sunk so deeply that the whole nest is overhung. Hummock nests (17), placed on the sides of hummocks, are confined to the low, wet parts of the valley that remain wet most of the summer, leaving only the dry exposed hummocks available for nest sites.

The six nests Wynne-Edwards (1952) reports on Baffin Island all faced between SW and SE. On my study area 87 per cent of the nests faced between W and NE with the highest number (28 per cent) facing N. This orientation relates directly to the prevailing winds, which during the breeding season are mainly from the S and SW. All 16 Horned Lark nests I

found on the study area had a protective clump of vegetation or rock on the S to W side of the nest (Verbeek, 1967).

Soper (1946), Pickwell (1947), Bent (1950), Sutton and Parmelee (1954), and Drury (1961) all agree that only grass is used in nest construction. None of these authors report the use of hair or feathers for lining of the nest. Of my 99 nests 16 contained horsehair, and one of these also had porcupine (*Erethizon dorsatum*) hair.

I never saw birds prospecting for a suitable nest site, but clearly the site is improved by actual excavating. Of 21 nests I found before they contained eggs, five had no nest material either; they were shallow scrapes in the ground with the excavated material at the entrance. I do not know which sex does the excavating or whether it is a joint effort. The first nest material is deposited in the form of a ring, so that both the bottom and the rim are bare earth. In the next phase this ring is widened slowly to the bottom and the top. In this state the nest looks finished but it probably is not, for about 2 more days pass before the first egg appears. Excavation time is unknown, but from the time the nest hollow is excavated to the day the first egg is laid usually takes 4 to 5 days.

In two instances nests of 1963 were reused in 1964. Both these nests became snow-free 23 June 1964 and contained the first eggs on 27 and 28 June, which shows how quickly after the snow disappears the breeding cycle can begin. At least one of these birds built her nest from the start, because the old nest material was almost gone. The condition of the other nest was not checked. In one of two other nests on pre-1963 sites the bird removed all old nest material before building the new nest, but in the other the nest material was not removed, and it became quite bulky.

Only once did I see a female carrying nest material. She was in the nest when I approached and the male circled around me. After about a minute she left the nest and the pair flew away together. On returning the female carried a beakful of grass and the male brought nothing, suggesting that only the female builds the nest.

I saw symbolic nest-building several times in 1964. A pair I watched on 21 June both had pieces of grass in their bills at 08:45, although the female had more. They kept close together and made much noise. After they had walked around for about a minute, they dropped the grass and began feeding. At 09:21 I saw a female with a grass stem in her beak that she dropped a moment later. The male was nearby but did not collect any grass. On 23 June I noticed another male with grass stems in his bill while the female fed about 20 m away. The frenzy, especially in the male, and the particular sound (not recorded) that accompanies this behavior ap-

TABLE 2  
 SIZE OF COMPLETE CLUTCHES OF THE WATER PIPIT ON THE BEARTOOTH PLATEAU

Clutch size	Number of clutches			
	1963	Per cent of total	1964	Per cent of total
3	2	6	4	8
4	14	38	8	16
5	19	51	34	78
6	2	6	4	8

pears to stimulate the female to start nest construction. Macdonald (1968) reports similar behavior in the Meadow Pipit.

### EGGS

The eggs were laid between 05:00 and 06:30, at daily intervals with only three exceptions. One female skipped a day between her first and second eggs while two others skipped one between their second and third eggs, in each case for no apparent reason.

The average fresh weight of 63 eggs in 1963 was 2.25 g (SE 0.029, range 1.84–2.84); 66 eggs in 1964 averaged 2.31 g (SE 0.014, range 2.10–2.60). The difference between mean weight in the two years is significant at the 0.05 per cent level ( $t = 2.129$ ).

Of the 99 nests found, 87 had completed clutches (Table 2). The average clutch size was 4.57 in 1963 and 4.76 in 1964. The difference between these means was not significant ( $t = 1.243$ ), but there was a significant shift toward larger clutches in 1964 (chi-square 18.41).

The average size of completed clutches grouped in 9-day periods (13–21 and 22–30 June; 1–9 and 10–18 July) remained rather stable in June and

TABLE 3  
 CLUTCH SIZE OF THE WATER PIPIT IN NORTH AMERICA WITH RESPECT TO LATITUDE

Latitude	Clutch size					Total	Mean	SE
	3	4	5	6	7			
35–45 <sup>1</sup>	7	25	64	8		104	4.70	0.029
45–55		5	9	1		15	4.73	0.084
55–65		2	4	6	1	13	5.46	0.115
65–75 <sup>2</sup>	1	1	17	19	2	40	5.50	0.054

<sup>1</sup> Including 87 clutches of this study.

<sup>2</sup> Including 20 clutches between 65–67° N.

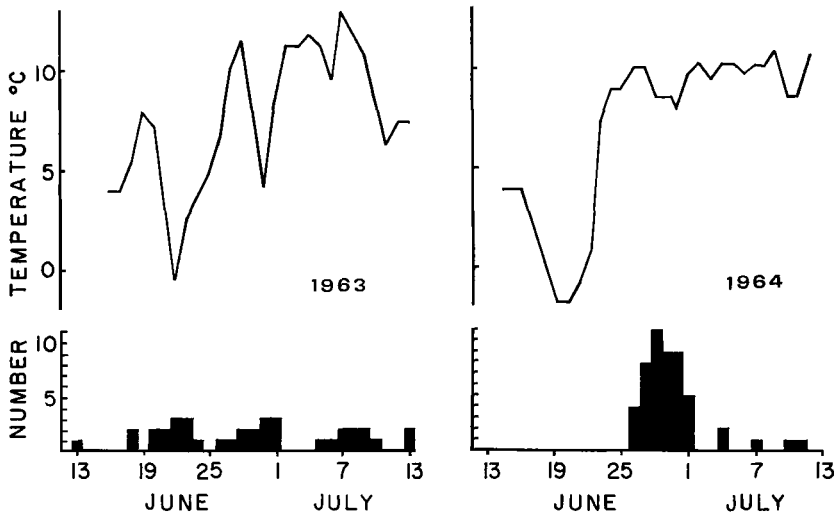


Figure 2. Relationship between mean air temperature and number of first eggs laid.

early July and dropped off toward mid-July: 4.67 ( $N = 14$ ), 4.64 ( $N = 14$ ), 4.64 ( $N = 13$ ), and 3.80 ( $N = 3$ ) in 1963, and zero eggs, 4.71 ( $N = 24$ ), 4.91 ( $N = 23$ ), and 4.00 ( $N = 3$ ) in 1964. Clutches were considered to belong in the period in which most of the eggs were laid.

Coulson (1956) shows larger clutches for the Meadow Pipit in the north (Norway) than in the south (Great Britain). An analysis of data in the North American literature and from the files of the Pacific and the Alaska nest record schemes shows a similar trend (Table 3). Only completed clutches are included. A complex of factors appear to explain this phenomenon. Pipit territories in the arctic are larger than in the alpine farther south; this produces a sparser population, less interference between pairs, and a decreased expenditure of time and energy on territorial defense, thus making more energy available for egg production. Moreover nestlings and fledglings are subject to greater mortality in the arctic (Sutton and Parmelee, 1954), so that more food is available for those pairs whose broods survive, perhaps because they built a better, more secluded nest. Also in the longer arctic day length parents can find more food for the young.

#### TEMPERATURE AND THE ONSET OF THE BREEDING CYCLE

I used two criteria to determine the day the first egg was laid: 1) if a nest was found with an incomplete clutch, the day the first egg was laid could be calculated, assuming a daily interval of laying; 2) if the day of



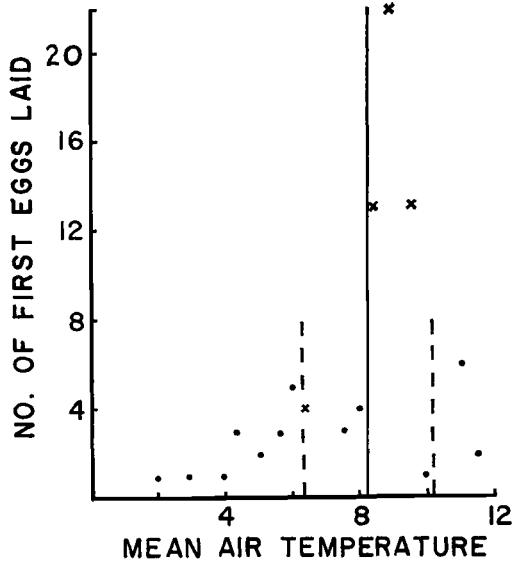


Figure 3. Relationship between number of first eggs laid and mean air temperature for the 4 preceding days. The solid line is the average temperature (8.2°C). The broken lines indicate one standard deviation. Dots are 1963 records and crosses are 1964 records.

hatching was known, the day the first egg was laid could be calculated by counting back 14 days for incubation plus 3-6 days, depending on the clutch size. No partial predation was assumed to have occurred. The distribution of first eggs laid could be established in 89 cases. A striking difference between both years is apparent (Figure 2). In 1963 the pattern spread out from 13 June to 13 July with three peaks, while 1964 had only one large peak. In the period from 26 June to 1 July 1963, 12 or 32 per cent of all first eggs were laid, while 89 per cent of all first eggs were laid in the same period in 1964.

Figure 2 also shows the average (mean of max. and min.) daily standard shelter temperatures. Most first eggs are laid about 4 days after a rise in temperature, apparently the time required for the egg to form. Fewer first eggs are laid after a drop in temperature. In 1964 temperatures were initially too cool, but when they increased and remained high, 89 per cent of all clutches were started within 6 days. As eggs are laid daily, apparently once egg formation starts the bird is committed to laying, which accounts for the egg peaks at low temperatures. The three females who skipped laying one day each did not do so because of low temperatures.

Kendeigh (1963) shows that the day of laying of the first egg in the

House Wren (*Troglodytes aedon baldwini*) is determined by the average temperature for the 3 days preceding its laying. He found an average temperature of 14.8°C (SD 2.7°C). I instead took the average temperature for the 4 days preceding the laying of the first egg, which gave a smaller standard deviation than the averages of 3 or 5 days. Also, as mentioned, it took about 4 days to build the nest. This average temperature was 8.2°C (SD 1.9°C) (Figure 3). The average temperature for the House Sparrow (*Passer domesticus*) is about 10°C and for the Tree Sparrow (*Passer montanus*) about 10°C at Oxford, England (Seel, 1968), and about 9.5°C at Warsaw, Poland (Pinowski, 1968). My value of 8.2°C may well be an overestimate, influenced by the many high temperatures of 1964. In any case, of the four species mentioned here, the pipit lives in the coolest climate and its laying temperature threshold would be expected to be the lowest.

As noted earlier, the average clutch size in 1964 was larger (4.76) than in 1963 (4.57). While in 1963 clutch size varied mainly between four and five eggs, in 1964 five-egg clutches far out numbered all others. Besides the significantly larger clutch size in 1964 there was also a slight but significant increase in egg weight. The increases in clutch size and egg weight are probably the result of the birds having more productive energy, either because more food was available, or because higher temperatures lowered energy requirements for existence.

#### INCUBATION

Pickwell (1947) notes an incubation period of "a full twelve days," while Sutton and Parmelee (1954) report "at least 11 days, 23 hours, and 15 minutes and almost certainly longer, since when we found the nest the clutch was complete." The incubation period of the Rock Pipit (*A. s. petrosus*) is about 14 days (Witherby et al., 1943).

The incubation period could be calculated for nine nests. Because eggs are laid in the morning between 05:00 and 06:30, last eggs found later than 06:30 were considered to have been laid at 05:45. In three closely watched nests, eggs hatched at about 2-hour intervals. Therefore when the last egg was found hatched more than 2 hours after the other eggs in the clutch had hatched, a correction was made. These corrections are rather crude, but necessary to obtain reasonably accurate estimates. The average incubation period was 14 days, 10 hours. One female, whose eggs never hatched, incubated for 19 days before she abandoned the nest.

As Sutton and Parmelee (1954) state, only the female incubates. During a total of 49 hours in a blind at two nests, I saw only females in-

TABLE 4  
MEAN ATTENTIVE AND INATTENTIVE PERIODS OF THE WATER PIPIT

Nest no.	Mean attentive (min)		Mean inatt. (min)		Mean inatt. male feeds female (min)		Mean inatt. female feeds herself (min)	
		SE		SE		SE		SE
19	12.9 (47)	1.1	5.6 (33)	0.6	4.2 (35)	0.6	8.4 (18)	1.5
67	17.7 (27)	1.9	5.8 (29)	1.4	4.4 (15)	3.2	7.9 (14)	0.7

cubating. The brood patch of the female is very conspicuous; 10 males shot away from the study area between 25 June and 20 July showed no broodpatch.

During incubation the male feeds the female at some distance from the nest. When he comes to feed, he gives a "tjueet" call and she answers "peet" from the nest. He repeats his call until the female flies toward him, calling "wee-wee-wee-wee." She continues calling while she lands in front of him and her display culminates in a frenzy of wing vibrations. He then feeds her, and she usually walks back to the nest, feeding on the way. If she flies back she calls "peet-peet," always lands 1 to 2 m away from the nest, and sneaks in from there.

When the female leaves the nest without invitation from the male, she stays off the nest longer, for an average of 8.14 minutes as against 4.28 minutes when the male feeds her. Thus feeding by the male shortens the female's inattentive periods. The average length of the mean inattentive period is very similar for both nests, but the average attentive period is much different (Table 4). One female was fed or fed herself on the average once every 16.60 minutes (12.00–24.00 minutes). Her mate fed her twice as often as she fed herself. The other female took food every 27.32 minutes (14.58–46.00 minutes) and the male fed her only about as often as she did herself, which explains the much longer mean attentive period (Table 4).

#### THE NESTLING STAGE

Sutton and Parmelee (1954) report the nestling period of one nest as "at least 12 days, at most 14 days" and from Johnson's (1933) paper I estimate a period of about 13 days. In this study the nestling period is the time between the hatching of the first egg (not necessarily egg No. 1) and the time the last nestling leaves the nest (again not necessarily the nestling hatched from the last egg laid). I made the following assumptions: When the nestling was still wet it was considered to have hatched at the

TABLE 5  
WEIGHTS IN GRAMS OF NESTLING WATER PIPITS

Age of nestling	N	Mean weight	Range	Mean change in weight
1	5	2.5	2.0- 2.8	
2	5	3.8	3.2- 4.2	+1.3
3	5	5.4	4.3- 6.1	+1.6
4	5	7.6	6.8- 8.2	+2.2
5	5	9.9	9.1-11.0	+2.3
6	5	12.7	11.6-13.8	+2.8
7	5	15.1	14.4-15.8	+2.4
8	5	15.4	14.4-16.2	+0.3
9	5	16.8	15.7-18.1	+1.4
10	5	18.9	18.1-19.6	+2.1
11	5	18.7	18.2-19.6	- 0.2
12	4	17.9	17.2-18.5	- 0.8
13	4	18.2	18.0-18.4	+0.3
14	3	18.6	17.8-19.2	+0.4

time I found it. When the nestling was already dry I considered it to have hatched 2 hours earlier. Whenever there were two or more nestlings, the time the first egg hatched was set back 2 hours times the number of nestlings. As nestlings left the nest mainly in the morning, I considered noon the last time of nest departure, unless I knew this to have happened earlier. The average nestling period of 41 nests was 14 days, 11 hours.

The nestlings are brooded by the female during the first few days, while the male does most of the feeding. In both years I recorded whether the female flushed from a nest or whether she was absent when I approached. In daily visits to each of 54 nests for which I have this information for the whole nestling period, 74 per cent of the females were present on the nest on day 1, 61 per cent on day 2, and 50, 56, 30, 22, and 6 per cent on days 3 to 7. After the 7th day females no longer brooded. The nestlings are brooded regularly until the 4th and 5th day; for the next few days the female is on the nest only to shelter the nestlings from rain or sun.

I weighed the five nestlings of one nest daily between 05:00 and 06:30 (Table 5). Toward the end of the nestling period two young left the nest prematurely. The average weight of 20 adults taken near the study area was 21.2 g (10 males 21.8 g; 10 females 20.6 g).

Table 6 shows when the eyes opened and when the primaries and secondaries broke their sheaths, and compares these results with those of the Meadow Pipit (Davies, 1958). The young reacted to my voice when they were 3 days old and to movement of my hand over the nest when 6 days old. They no longer reacted to these stimuli when 7-8 days old, and they crouched deeper in the nest when 9-10 days old. The

TABLE 6  
DEVELOPMENT OF THE WATER PIPIT AND THE MEADOW PIPIT COMPARED

Species	No. of broods with eyes open at day			No. of broods with remiges out of sheaths at day			
	4	5	6	7	8	9	
<i>Anthus spinoletta</i>	22	12	1	7	21	9	(secondaries)
				0	19	14	(primaries)
<i>Anthus pratensis</i> <sup>1</sup>	3	3	1	1	12	2	(secondaries)

<sup>1</sup> Davies (1958).

nestlings could be handled until they were 12 days old, but thereafter usually left the nest.

The parents first removed fecal sacs when the young were 1 day old, and the rate of removal increased as they grew. In one nest (five nestlings) feces were removed at a rate of 1.5/hr when the young were 1 day old, 4.5/hr at 4 days, and 11.3/hr at 7 days. Feces were either eaten at the nest or carried away in the bill. Because the female spends most of her time on the nest during the first 4 days, the male removes proportionately more feces. After the brooding period is over both sexes remove feces at about equal frequency, at least to the 7th and last day recorded.

#### FLEDGLINGS

During the last few days of the nestling period the juveniles exercise their wings frequently while standing in the nest. When they leave the nest, the young are well-feathered and have short tails (see Shortt, 1951). Wynne-Edwards (1952) gives evidence that pipits leave the nest before they can fly, which I did not find in my study. One bird flew about 20 m from the nest when I approached it, and I was able to catch it only after it flew twice more. Thus fledglings can fly short distances when they leave the nest at 14–15 days of age.

The 222 nestlings that successfully fledged were color-banded at about 10 days of age. Only 19 of these were seen at least once after fledging, and 5 were seen a second time. Fledglings are hard to see because they are well camouflaged and hide until you come very close. They stay around the nest for about a week and then drift farther away. If a territory includes a rock slide or a stone stripe, young pipits are likely to be found there. Fledglings become independent of their parents about 14 days after leaving the nest.

#### BREEDING SUCCESS

*Reproductive rate.*—Reproductive rate is here understood as the number of eggs per nest per season (Table 7). Only those nests that contained at

TABLE 7  
SUMMARY OF WATER PIPIT BREEDING DATA

	1963		1964	
	Number	Per cent	Number	Per cent
Nests (all clutches) <sup>1</sup>	38		46	
Eggs laid	169	100.00	217	100.00
Eggs per nest	4.45		4.74	
Eggs hatched	109	64.50	177	81.57
Eggs hatched per nest	2.87		3.85	
Eggs not hatched	17	10.05	30	13.82
Eggs lost before hatching	43	25.45	10	4.61
Young fledged of eggs hatched	77	70.64	145	81.92
Young fledged per nest	2.05		3.22	
Young lost before fledging	32	29.36	32	18.08
Young fledged of eggs laid		45.56		66.82
Per cent of successful nests <sup>2</sup>		57.89		80.43

<sup>1</sup> Not including nests that were abandoned.

<sup>2</sup> Nests that produced at least one fledgling.

least one egg are included. The higher reproductive rate in 1964 results from an increased clutch size and a smaller loss of eggs to predators.

The Water Pipit has only one clutch per season. Renesting is difficult to establish, because this can only be determined with banded adults. Of two females banded in 1963 and breeding on the study area in 1964, one abandoned her nest and territory on 6 July and did not renest, at least not on the study area. Abandonment of the nest and of the territory usually go together, so that renesting birds would have to repeat all the preliminaries that precede nest construction, such as territory and nest site selection.

As the breeding cycle takes 49–52 days (from the beginning of nest construction to fledgling independence), there is a limit to renesting. In both years no new nests were begun after 8 July, although several nests were robbed or disturbed after this date. The young of nests initiated on 8 July fledged in the second week of August. In a late season such as 1964 the chances of renesting are very slight, but in an early season such as 1963 the possibility should not be excluded. The much reduced mean clutch size for the period 10–18 July may be due to higher temperatures and perhaps also to some replacement clutches.

*Survival and productivity.*—Survival is here defined as the number of eggs hatched and the number of nestlings fledged in the population (Table 7). Here too the 1964 season was more successful than the previous one. Only 2.87 eggs per nest hatched in 1963 versus 3.85 eggs per nest in 1964. The low hatching success in 1963 was mainly through egg loss, which amounted to 25.45 per cent of all eggs laid.

Productivity, or the number of young fledged of total eggs laid, for the

TABLE 8  
CAUSES OF LOSSES OF EGGS AND NESTLINGS

	1963			1964		
	N	No. of nests	Per cent	N	No. of nests	Per cent
<b>Eggs</b>						
Predation	39	13	63.93	10	4	28.57
Eggs broken <sup>1</sup>	2	2	3.28	0	0	
Buried by gopher <sup>2</sup>	2	1	3.28	0	0	
Nests deserted	18	5	29.51	25	5	71.43
<b>Total</b>	<b>61</b>		<b>100.00</b>	<b>35</b>		<b>100.00</b>
<b>Nestlings</b>						
Predation	16	5	50.00	21	6	65.63
Trampling by sheep	3	1	9.38	0	0	
Buried by gopher	3	1	9.38	0	0	
Parasites and disease	6	2	18.75	6	2	18.75
Unknown	4	1	12.50	5	5	15.63
<b>Total</b>	<b>32</b>		<b>100.01</b>	<b>32</b>		<b>100.01</b>

<sup>1</sup> Broken in handling.

<sup>2</sup> Pocket Gopher (*Thomomys talpoides*) digging.

two seasons averaged about 56 per cent (Table 7). Sutton and Parmelee (1954) report low productivity on Baffin Island of 21.74 per cent, which may have been slightly higher because they did not visit nests daily; from 69 eggs in 14 nests possibly 15 fledged.

*Mortality.*—Under this heading are included all known losses of eggs and nestlings. Egg losses are of two types: those lost to various causes listed in Table 8 and those lost through failure to hatch (infertility, arrested development, etc.).

I suspected that my weighing and measuring the eggs might have been responsible for the rather large number that failed to hatch in 1964 (Table 7). To determine the possible influence of handling the eggs on hatching success, I calculated the number of eggs weighed (79) in nests in which no other losses occurred and the number of eggs in these nests that failed to hatch (15). Similarly 20 of the 208 eggs that were not weighed failed to hatch, a hatching success of 90.38 per cent. By applying the per cent failure (9.62) of the nonweighed eggs to the number of weighed eggs, I calculated the excess loss in the weighed eggs. My handling of the eggs apparently caused the loss of eight eggs (one in 1963 and seven in 1964), certainly an insignificant portion of the total 386 eggs laid (Table 7).

Egg losses other than by failure to hatch are caused mainly by nest desertion and predation (Table 8). One female deserted a nest near one

where I was making a daily picture record of nestling feather development, apparently disturbed by my activities. Another nest was disturbed by frequent visits of tourists. Desertion was most frequent during egg laying and early in the incubation period. The birds never deserted nestlings, no matter how much time I spent around the nest.

Predation, probably by the deer mouse (*Peromyscus maniculatus*) and the long-tailed weasel (*Mustela frenata*), caused the greatest loss of eggs and nestlings (Table 8). The deer mouse was very plentiful during the summer of 1963 (Pattie and Verbeek, 1967). In seven cases of predation of eggs and nestlings in 1963 I put a live-trap in front of the nest and during the following night caught deer mice in four of them. Feathers strewn around several nests suggested a battle between the adult bird, probably the female, and the predator. In 1963 no adult females were known to have been killed on the nest. A few incompletely fragmented eggs showed that mice punctured them at the pointed end. In many cases, especially when the nestlings were too small to escape, all the young were killed and partly eaten. Table 7 shows that four times more eggs were lost in 1963 than in 1964, while the loss of nestlings was about equal in both years. It appears then, that the deer mouse is mainly an egg robber.

To what extent the long-tailed weasel was a nest predator in 1963 is unknown. Two weasels were known on the study area and, as one was seen carrying a vole for some distance, it may have had a litter. In 1964 we saw weasels more often and in larger numbers, up to five in one group. In all cases of predation in 1964 most eggs and all nestlings were gone from the nest and no chewed remains of nestlings were left, in sharp contrast to 1963. In addition I found two dead females in front of their nests, one bitten in the skull, the other with a punctured chest. Most nest material of nests robbed in 1964 was torn out, and I noticed the same thing in several nests I visited after the young had fledged. I saw no such nest destruction in 1963. In front of one of these nests I found a fresh weasel scat. Because of the small number of mice and the relative large number of weasels in 1964, I think that weasels were the main and perhaps the only mammalian predators of pipits in 1964, preying mostly on nestlings. With the decline of the mouse population, the weasels took more pipits, which to them are apparently a secondary preference to mice.

In 1963 four 11-day-old nestlings of one nest died of a blowfly larvae infection; one nestling in a nest of four died of the same cause in 1964. These were the only pipit nests in which blowflies were found, although 4 out of 11 Horned Lark nests in 1964 were infested (Verbeek, 1967). The species of fly is being described (Sabrosky, MS).



TABLE 9  
FEEDING RHYTHM IN ONE NEST WITH FIVE YOUNG

Age in days	Period of observation	Adjusted time (min)	No. of times male feeds	No. of times female feeds	Feeding rate/hr
0	06:03-06:50	40	4	0	6
0	09:12-11:42	127	11	5	7.6
1	13:27-14:49	40	5	1	9.0
4	15:00-17:00	113	12	9	11.2
7	16:57-18:27	79	10	11	16.0

### FOOD

As the female broods the nestlings intensively during the first 4-5 days, the male brings food more often than she does during this period (Table 9). After the first 4-5 days both parents visit the nest equally often. Feeding rates in Table 9 are calculated from an "adjusted observation time," which is that part of the total period spent in the blind starting from the moment of the first feeding till the end of the period. These show an increase in feeding rate with nestling age, which Johnson's (1933) data do not reveal. She also mentions that "rain and fog did not seem to retard feeding activities of the parent birds," but during one rain and hailstorm I saw 4-day-old young being brooded by the female and neither parent fed them for a total of 44 minutes.

During the brooding period the male gives all or part of the food he brings to the nest to the female, and she gives it to the young. During this period the female leaves the nest at times, apparently to feed herself, because on her return to the nest she does not always feed the nestlings. If the female is gone when the male comes to the nest, he feeds the young himself. After the brooding period the male feeds the young directly at all times.

Two other species, the Horned Lark and the White-crowned Sparrow (*Zonotrichia leucophrys*), breed on the study area. The latter did not breed on the area in 1964 and there were only two nests in 1963. A fourth species, the Black Rosy Finch (*Leucosticte atrata*) nests in the cliffs surrounding the study area and only uses the area to feed. All four species were present when I arrived each June. The three nesting species differ in habitat and in nest site selection, although some overlap occurs. Segregation of all four species is also accomplished by feeding habits and by the type of food eaten.

Martin et al. (1951) report stomach contents of about 1 per cent plant material in 45 adult Water Pipits, the rest being insects. On the Bear-

TABLE 10  
FEEDING RATE OF THE WATER PIPIT AND THE HORNED LARK ON SNOW AND  
AMONG VEGETATION

Species	On snow			Among vegetation		
	N	Pecks/min	Range	N	Pecks/min	Range
Water Pipit	9	43.1	32-59	5	7.8	1-19
Horned Lark	3	38.3	33-49	2	21.0	19-23

tooth Plateau, 51 adult birds and 11 fledglings had stomach contents of almost 100 per cent insects and a trace of plant material consisting of hard seeds. The stomach content of 25 nestlings (4-14 days old) consisted of insects and grit. In the field I first noticed the presence of grit in the feces of the nestlings. Grit did not occur in stomachs of nestlings younger than 4-5 days old. On the average nestlings had more grit (0.12 g, N = 25) than the adults (0.02 g, N = 51). Two nestlings had 0.35 and 0.46 g of grit; in addition to this grit, mainly quartz, two stomachs contained grit-sized balls of silver paper, and in three other nestlings I found microtine molars and a sciurid molar. Grit was also found in the stomachs of adult and nestling Horned Larks (Verbeek, 1967).

As Drury (1961) notes, pipits in general feed in thicker, moister vegetation, while larks feed in drier sites. Pipits feed regularly along stream banks and on occasion may be seen feeding shank-deep in water. Larks are not found in such situations and they tend to avoid dense vegetation. The summer diet of three Horned Larks at Indian Harbor, Labrador, consisted of 52 per cent insects and 48 per cent seeds (Cottam and Hanson, 1938). Martin et al. (1951) report 67 per cent plant material in 34 summer birds. On the Beartooth Plateau, 12 adult Horned Larks taken between 14 June and 1 September contained 78 per cent insects and 22 per cent seeds, while six nestlings in July contained 100 per cent insects (Verbeek, 1967).

During the spring pipits and larks feed extensively on, rather than at the edge of snow fields. It is perhaps of significance that both species have a long hallux and a walking gait, rather than the short hallux and hopping gait of the two fringillids. The presence of wind-blown insects on high altitude snow fields has been known for a long time (Mani, 1962). On days with much sunshine and moderate winds I found many dead or numbed insects on the snow. The number of insects increases with continuous favorable weather, but subsequent strong winds remove many or all of them.

To determine the importance of snow fields in the feeding economy of these two species, I counted the number of pecks per minute the birds

made on snow and among vegetation (Table 10), assuming that with each peck one food item is consumed. Although the samples are small, they do show a trend. That food is easier to obtain on the snow than among the vegetation is borne out by the feeding behavior. On the snow the birds run from one readily visible food item to the next; in the vegetation both species walk slowly when foraging. Obviously snow fields can be of importance to the birds' energy budget by letting them spend less energy on self maintenance and more on such reproductive activities as territorial defense. It is thus probably advantageous for a pair of pipits to have at least part of a snow field in their territory.

Early in the spring the Black Rosy Finches feed along the edges of the melting snow fields. Very seldom do they forage on the snow itself, and if they do, only near the edge. Continued thawing exposes a steady supply of food that is easily seen because the ground near the snow is still free of new vegetation. Later when the snow is gone, the finches feed in sparsely vegetated areas near the cliffs. Very few occurred on the study area. The stomachs of 70 adult birds collected from June to August in western Wyoming, Montana, and northern Utah contained 97 per cent seed and 3 per cent animal matter (French, 1959). French also notes that though young are fed mainly insects, by the time they are 9 days old they begin to receive some seeds, and at fledging seeds form the main diet with a few insects. As the nestlings remain in the nest for about 18-20 days, and as adults gather food for the young in habitats other than those used by pipits, competition for insects is insignificant.

White-crowned Sparrows were never seen on the snow. On my arrival in 1963 the willow patches and parts of the hummocks were partially snow free. The sparrows fed along the runoff channels and in the marshy vegetation throughout their stay.

In summary the Water Pipit has little competition for food from the Black Rosy Finch and the White-crowned Sparrow, both of which are seed eaters as adults. While both species feed their young insects, the finches did not forage in the study area when they had nestlings, and so few sparrows were present the number of insects they took was negligible. The Horned Lark is less dependent on insects than the Water Pipit, but still takes more than 70 per cent of its diet in the form of animal matter and feeds its young entirely with insects. Competition between the latter two species is lessened by foraging in different habitats.

#### POSTBREEDING PERIOD

When the individual family groups begin to break up about 2 weeks after fledging, loose associations develop among pipits. Typical flock behavior becomes stronger toward early September, but I saw lone birds

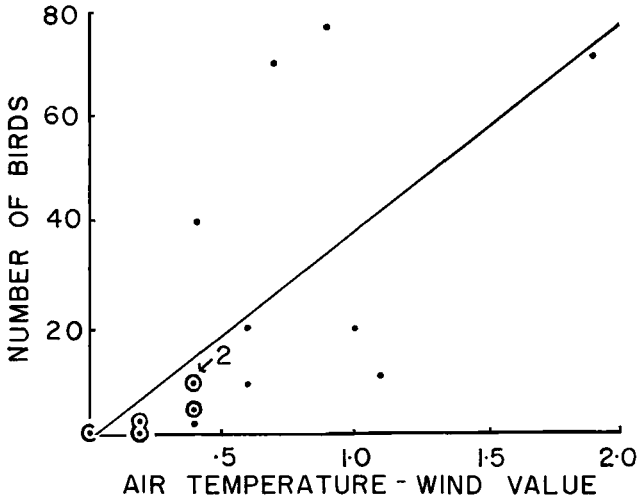


Figure 4. Relationship between the air temperature-wing value (see text) and the number of Water Pipits on the study area from 16 August to 22 September 1963 ( $N = 15$ ). Snow cover is indicated by circles. Regression equation  $y = 38.64x - 0.69$ .

till the end of my stay, 22 September 1963. While the adults are molting in mid-August the flocks are composed mainly of juveniles, but by the end of August the adults are flocking with the young of the year.

As banded fledglings and adults are seldom seen again, possibly when young become independent the local population or part of it moves away (south ?) and is replaced by other birds, a postulate supported by the presence of many unbanded juveniles in the late summer flocks.

The alpine environment is often likened to the arctic because of such similarities as a short summer and low vegetation. One fundamental difference between the arctic and the alpine is the fact that alpine birds can quickly escape sudden unfavorable climatic changes by a short vertical migration. To determine why the study area contained more pipits on certain fall days than on others, I made a census at irregular intervals along a route of about 2 km, which took about 1 to 1½ hours and traversed all habitats. I counted all pipits that flushed on either side of me, regardless how far away they were. As pipits usually do not flush unless one is within perhaps 30 m of them, the method was essentially a strip census. Figure 4 shows the number of birds seen against a quotient derived from air temperature and wind speed at 18 inches above ground (mean temperature divided by kilometers of wind per hour). The number of birds present is significantly dependent on air temperature and wind velocity ( $t = 3.095$ ).

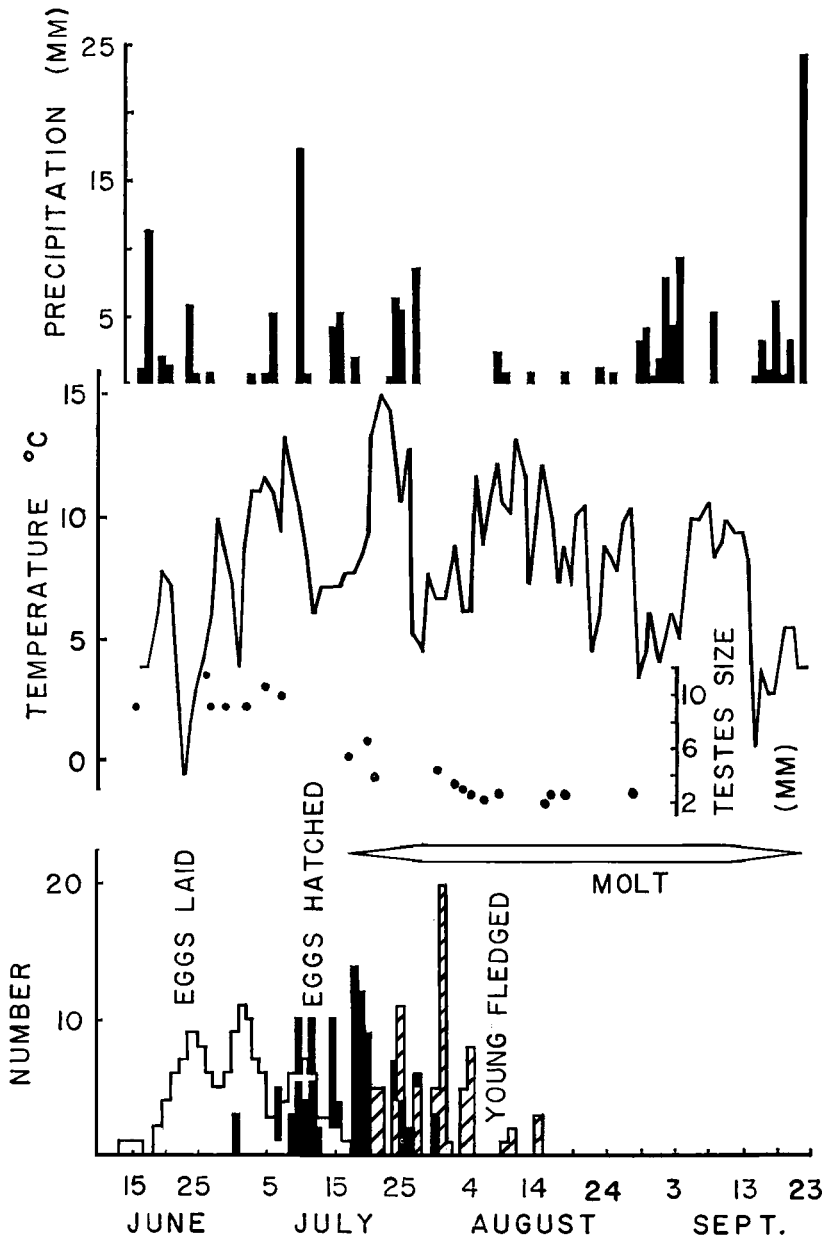


Figure 5. Schedule of the breeding cycle and the period of molt of adult birds plotted against mean air temperature and precipitation in 1963.

More birds are present at high air temperatures, low wind velocities, and absence of a snow cover than under opposite conditions. I do not know how long the pipits stayed on the study area after I left, but I assume that the onset of persistent snow cover forces them to leave. I saw no pipits on the study area nor on the Beartooth Plateau in general during 3 days I spent there from 28 to 30 December 1963.

#### THE BREEDING CYCLE AND THE ALPINE ENVIRONMENT

The alpine summer is short, running roughly 2½ months from mid-June to late August and early September. Only during this period is the weather relatively stable and dependable, with mean temperatures remaining above freezing and persistent snow absent (Figures 5 and 6). Ambient temperatures at ground level are very high because of intense solar radiation, which accelerates the growth of plants and the rapid development of the insect fauna. Thermal winds bring large numbers of insects to the alpine zone from lower elevations, which is of importance to the pipits during the first weeks before the indigenous insects increase in numbers. The ability of the pipits to utilize this food source allows them to set up territories early, so that this time- and energy-demanding period can be largely completed prior to nest construction, when the snow melts.

Exactly when the pipits arrive on the breeding ground is unknown, but both sexes apparently arrive physiologically ready to begin the breeding cycle. This permits quick action once conditions become favorable. Territories are established, sometimes when the ground is still covered with snow, in areas that become snow-free early (Figure 1). Nests are sunk in the ground or vegetation, which is typical of the genus, but the almost exclusive orientation away from the prevailing wind must be considered a special adaptation against wind and drifting snow. The reuse of old nests is advantageous, especially when little new nest material need be added. On the other hand, in the few cases of reuse of old nests, these were the first places to become clear in territories otherwise still covered with snow. Whatever nest site becomes available first depends on the pattern of snow deposition (drifting), and the reuse of old nests is probably fortuitous.

The laying of the first egg is triggered by a mean air temperature of 8.2°C for 4 days. A low threshold temperature allows for an earlier start of the breeding cycle, which requires about 50 days from nest building to independence of the young. The season of about 80 days of suitable weather conditions allows little leeway. If the threshold temperature were higher, the eggs would hatch during the height of the adult molt. A lower threshold temperature could lead to disaster during the unsettled weather of early June. When the threshold level is reached, breeding activities

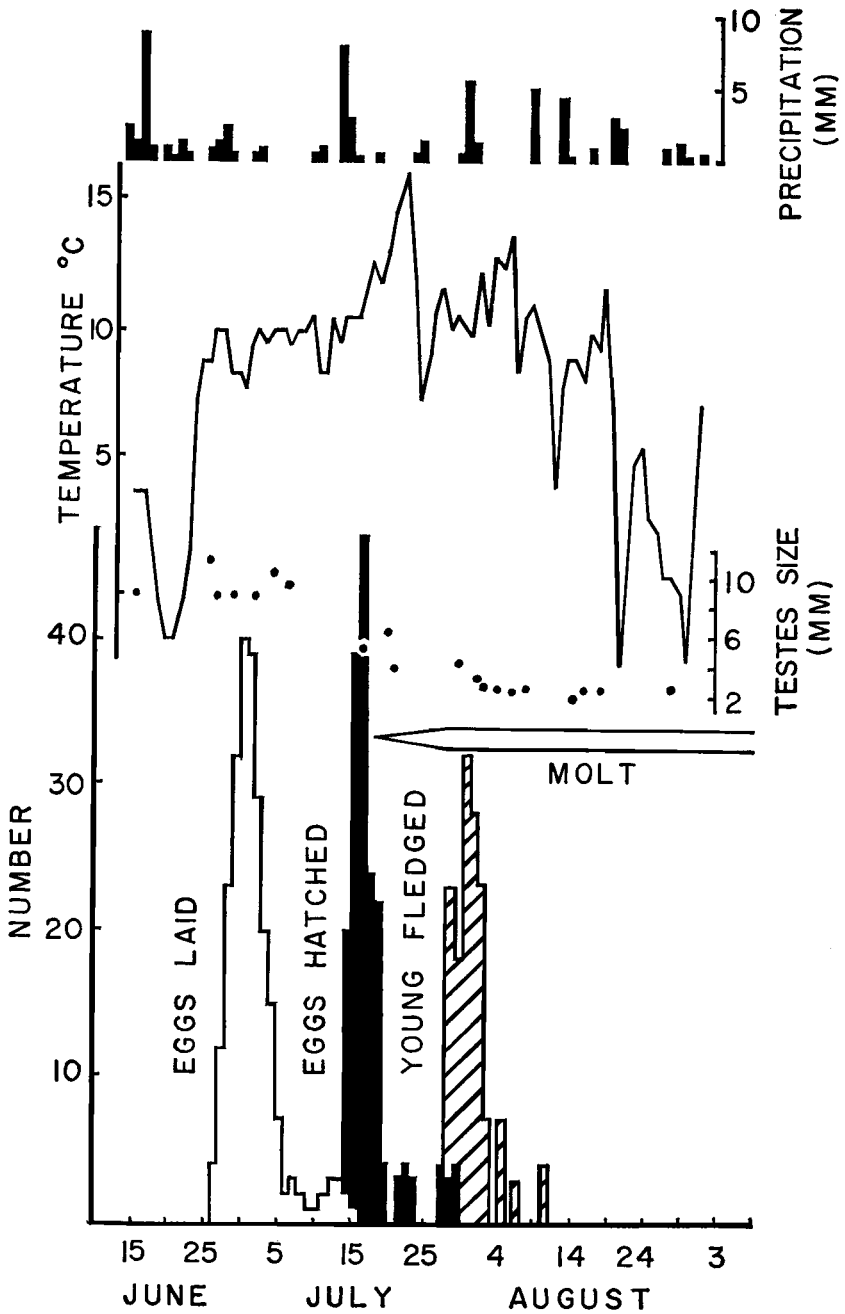


Figure 6. Schedule of the breeding cycle and the period of molt of adult birds plotted against mean air temperature and precipitation in 1964.

start immediately and both sexes in the entire population respond in unison (Figure 6).

The earliest traces of the postnuptial molt appear in mid-July (Figures 5 and 6). The males begin to molt their flight feathers the first week of August, followed by the females about 2 weeks later. Thus the molt starts when most young are still in the nest and reaches its height when the young become independent. It is apparently advantageous for the adults to molt in the alpine right after breeding rather than at lower altitudes later on. Insufficient data on insect abundance indicate that most food is present in the second half of August. This telescoping of the breeding effort and molt are a necessity of the short season. By the first week in September both adults and juveniles are ready for the onset of bad weather and the fall migration.

Some of the adaptations listed above have been mentioned also for arctic Water Pipit populations (Wynne-Edwards, 1952; Irving, 1960b; Drury, 1961) and for the Meadow Pipit (Davies, 1958). Wynne-Edwards (1952) found eggs in a clutch hatching over 3–4 days. Sutton and Parmelee (1954) found no evidence of this in two nests followed in some detail, although from the size variation in a brood of six in another nest, they inferred that incubation had begun well before the clutch was completed. Gross (1932) believed incubation to start with the laying of the last egg. I found neither evidence for a prolonged hatching period nor for size variation among nestlings in any brood. Lastly, Wynne-Edwards mentions a "notable absence of territorial disputes," but Drury (1961) does not appear to agree with this and I find no evidence of it in the alpine.

#### ACKNOWLEDGMENTS

First and foremost I wish to thank R. S. Hoffmann for his interest in this study, his help and editing of the manuscript. For their special interest, shown in frequent discussion and help given, I thank P. L. Wright, R. W. Fields, and M. D. F. Udvardy. Special thanks are due to D. L. Pattie and C. I. Fudge for their companionship in the field.

I gratefully acknowledge a grant from the Frank M. Chapman Memorial Fund of the American Museum of Natural History and a Louis Agassiz Furtres Research Grant from the Wilson Ornithological Society. I also wish to acknowledge funds from National Science Foundation Grant no. B 14089 directed by R. D. Taber and R. S. Hoffmann.

#### SUMMARY

The breeding ecology of the Water Pipit was studied on 116 hectares of alpine tundra of the Beartooth Plateau, Wyoming 45° N, 109° 30' W, elevation 3,200 m, from 14 June to 21 September 1963 and from 12 June to 20 August 1964.



On arrival in spring pipits occupy snow-free areas having tussocks, tilted rocks, or eroded places. In 1963 and 1964 I found 47 and 52 nests respectively; the study area probably had about 60 nests both years. Population density was about 0.5 pair per hectare. The mean territory size of five pairs was 1,810 square meters. Nests are sunk in the ground and partially overhung by vegetation, sod, or rock. The nest entrance faces away from prevailing winds. The female builds the nest of grasses and some hair in about 4–5 days.

The average fresh weight of 63 eggs in 1963 was 2.25 g and of 66 eggs in 1964 was 2.31 g. Average size of completed clutches was 4.57 in 1963 and 4.76 in 1964. It is suggested that average egg weight and clutch size were larger in 1964 because of more productive energy available either from greater food availability, or from lower existence energy requirements with higher temperatures.

The mean incubation period was 14 days, 10 hours. Only the female incubates. During incubation the male feeds her at some distance from the nest. When fed by the male the average inattentive period was 4.28 minutes, but when the female left the nest to find food for herself the average inattentive period was 8.14 minutes.

The mean nestling period was 14 days, 11 hours. Nestlings are brooded until the 4th or 5th day, after which the female only shades them and protects them from rain. Eyes open at 4–5 days, and primaries and secondaries break their sheaths at 8–9 days. Fecal sacs are eaten or carried away by both parents.

The reproductive rate was 4.45 eggs per nest in 1963 and 4.74 eggs per nest in 1964. Apparently only one clutch is laid per season. Possible renesting is limited by the short alpine summer, which is little longer than the 50 days needed for the total breeding cycle from nest building to independence of young. Hatching success was 90.38 per cent. Survival to the fledgling stage was 2.05 young per nest in 1963 and 3.22 young per nest in 1964. Mean productivity for the two seasons was 56 per cent.

Most mortality was from predation of eggs and nestlings. The deer mouse was the main predator in 1963, the long-tailed weasel in 1964.

Both parents feed the nestlings on insects only; nestling stomachs contain grit in larger amounts than found in the adults. Feeding rate increases with the nestlings' age.

Loose flocks composed mainly of juveniles form in mid-August, when the adults undergo the postnuptial molt. Adults join the flock by the end of August. Periodic vertical migration is initiated by strong winds, low temperatures, and snow cover.

## LITERATURE CITED

- BENT, A. C. 1950. Life histories of North American wagtails, shrikes, vireos and their allies. U. S. Natl. Mus., Bull. 197.
- BAMBERG, S. A. 1961. Plant ecology of alpine tundra areas in Montana and adjacent Wyoming. Unpublished M.S. thesis, Boulder, Univ. Colorado.
- COTTAM, C., AND H. C. HANSON. 1938. Food habits of some arctic birds and mammals. Field Mus. Nat. Hist., Zool. Ser., 20: 405-426.
- COULSON, J. C. 1956. Mortality and egg production of the Meadow Pipit with special reference to altitude. Bird Study, 3: 119-132.
- DAVIES, S. J. J. F. 1958. The breeding of the Meadow Pipit in Swedish Lapland. Bird Study, 5: 184-191.
- DRURY, W. H., JR. 1961. Studies of the breeding biology of the Horned Lark, Water Pipit, Lapland Longspur, and the Snow Bunting on Bylot Island, Northwest Territories, Canada. Bird-Banding, 32: 1-46.
- FRENCH, N. R. 1959. Life history of the Black Rosy Finch. Auk, 76: 159-180.
- GIBB, J. 1956. Food, feeding habits and territory of the Rock Pipit (*Anthus spinoletta*). Ibis, 98: 506-530.
- GROSS, W. 1932. Home life of the American Pipit. Bird-Lore, 34: 309-314.
- HANZÁK, J. 1958. Zur Ökologie der Gebirgsvögel in der Tschechoslowakei. Proc. 12th Intern. Ornithol. Congr., 1: 294-298.
- IRVING, L. 1960a. Nutritional conditions of Water Pipits on arctic nesting grounds. Condor, 62: 469-472.
- IRVING, L. 1960b. Birds of Anaktuvuk Pass, Kobuk and Old Crow. U. S. Natl. Mus., Bull. 217.
- JOHNSON, H. S. 1933. Notes on the family life of a pair of American Pipits. Wilson Bull., 45: 114-117.
- JOHNSON, P. L., AND W. D. BILLINGS. 1962. The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. Ecol. Monogr., 32: 105-135.
- KENDEIGH, S. C. 1963. Regulation of nesting time and the distribution in the House Wren. Wilson Bull., 75: 418-427.
- MACDONALD, D. 1968. Meadow Pipit display. Scottish Birds, 5: 176.
- MANI, M. S. 1962. Introduction to high altitude entomology. London, Methuen.
- MARTIN, A. C., H. S. ZIM, AND A. L. NELSON. 1951. American wildlife and plant. New York, Dover Publ., Inc.
- NIMLOS, T. J., AND R. C. MCCONNELL. 1962. The morphology of alpine soils in Montana. Northwest Sci., 36: 99-112.
- NIMLOS, T. J., R. C. MCCONNELL, AND D. L. PATTIE. 1965. Soil temperature and moisture regimes in Montana alpine soils. Northwest Sci., 39: 119-138.
- PATTIE, D. L., AND N. A. M. VERBEEK. 1966. Alpine birds of the Beartooth Mountains. Condor, 68: 167-176.
- PATTIE, D. L., AND N. A. M. VERBEEK. 1967. Alpine mammals of the Beartooth Mountains. Northwest Sci., 41: 110-117.
- PICKWELL, G. 1947. The American Pipit in its arctic-alpine home. Auk, 64: 1-14.
- PINOWSKI, J. 1968. Fecundity, mortality, numbers and biomass dynamics of a population of the Tree Sparrow (*Passer m. montanus* L.). Ekologia Polska., Ser. A., 16: 1-58.
- RINGLEBEN, H. 1957. Bergpieper (*Anthus s. spinoletta* (L.)) in Niedersachsen. Ber. Naturh. Ges. Hanover, 103: 91-100.

- SEEL, D. C. 1968. Breeding seasons of the House Sparrow and the Tree Sparrow *Passer* spp. at Oxford. *Ibis*, 110: 129-144.
- SHORTT, T. M. 1951. On the juvenile plumage of North American pipits. *Auk*, 68: 265.
- SOPER, J. D. 1946. Ornithological results of the Baffin Island expeditions of 1928-1929 and 1930-1931, together with more recent records. *Auk*, 63: 418-427.
- SUTTON, G. M., AND D. F. PARMELEE. 1954. Survival problems of the Water Pipit in Baffin Island. *Arctic*, 7: 81-92.
- VERBEEK, N. A. M. 1967. Breeding biology and ecology of the Horned Lark in alpine tundra. *Wilson Bull.*, 79: 208-218.
- WITHERBY, H. F., F. C. R. JOURDAIN, N. F. TICEHURST, AND B. W. TUCKER. 1943. *The handbook of British birds*, vol. 1. London, Witherby Ltd.
- WYNNE-EDWARDS, V. C. 1952. Zoology of the Baird expedition (1950). 1. The birds observed in central and southeast Baffin Island. *Auk*, 69: 353-392.

*Department of Zoology, University of Montana, Missoula, Montana 59801. Present address: Museum of Vertebrate Zoology, University of California, Berkeley, California 94720.*