The Condor 89:788–797
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DISTRIBUTION, STATUS, AND ORIGIN OF WATER PIPITS BREEDING IN CALIFORNIA[1]

JON H. MILLER
1034 Shattuck Avenue, Berkeley, CA 94707

MICHAEL T. GREEN
Department of Biology, University of North Carolina, Chapel Hill, NC 27514

Abstract. We investigated the racial identity, distribution, and abundance of Water Pipits (*Anthus spinoletta*) breeding in the mountains of California. This common nesting species of alpine tundra was not known to breed in California until the 1970s; a review of historical evidence suggests recent colonization. Mensural and plumage comparisons show California populations to be *A. s. alticola,* the breeding race of the Rocky Mountains. This is of biogeographical interest, because the abundant wintering and migratory pipit of California is *A. s. pacificus,* while *alticola* normally occurs hundreds of miles to the east. Water Pipits currently nest in mesic alpine vegetation throughout much of the southern and central Sierra Nevada. Breeding densities are highest and most uniform in the southernmost part of this range. The only known breeding population in California outside of the Sierra Nevada occurs on San Gorgonio Mountain in southern California. We hypothesize that the previous absence or rarity of breeding Water Pipits in the Sierra Nevada may be attributable to the most recent paleoclimatic xerothermic period, the Hypsithermal (ca. 5,000 to 2,900 years BP), which impoverished many alpine biotas of arctic-old cordilleran affinity. Climate and habitat differences may prevent *pacificus* from breeding in California, and geographic barriers may have hindered colonization by *alticola.* The occurrence and timing of the present colonization may be fortuitous. Alternatively, it is possible that prior colonization of Great Basin ranges by *alticola* facilitated eventual dispersal to the Sierra Nevada.

Key words: Water Pipit; Anthus spinoletta; *Sierra Nevada; historical status; colonization; biogeography; alpine.*

INTRODUCTION

The Water Pipit (*Anthus spinoletta*) is a principal and widespread member of alpine avifaunas in western mountain ranges that support mesic alpine tundra. However, this species was not known to breed in the Sierra Nevada of California until quite recently, and appears to have been rare or absent during the first half of this century. This prior absence is noteworthy, because the Sierra Nevada is among the largest mountain ranges in North America and contains extensive alpine habitat suitable for breeding Water Pipits. The recent discovery of breeding Water Pipits in the southern and central Sierra raises several questions of biogeographical interest, including the origin and racial identity of these birds.

The Water Pipit is holarctic in distribution, with two races breeding in arctic and alpine tundra in western North America. *Anthus s. alticola* breeds throughout the Rocky Mountains and outlying ranges from southern British Columbia and Montana (Verbeek 1970; Miller and Green, pers. observ.), south to New Mexico and Arizona (AOU 1957), and west to the eastern Great Basin ranges (Behle 1978; R. E. Johnson, unpubl.). The winter range of this taxon is not well known, but appears to be from southern Utah south to Mexico (Phillips et al. 1964, Hayward et al. 1976). A small number have been collected in coastal California during the spring migration (Swarth 1900, Grinnell and Miller 1944). *Anthus s. pacificus* breeds in the Pacific cordillera from the mountains of Oregon north to the alpine and arctic tundra of Alaska. This race winters in the Pacific states, east to the Rocky Mountains, and south to western Mexico (Grinnell and Miller 1944, AOU 1957, Phillips et al. 1964).

The fact that the Sierra Nevada lies entirely within the winter range and migration route of *pacificus,* while *alticola* was not known to regularly approach California at any time of the year, led to a natural assumption that newly discovered Sierran pipits were also *pacificus* (e.g., Parkes 1982). A critical determination of racial identity was lacking, however.

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[1] Received 27 October 1986. Final acceptance 31 March 1987.

In this paper we determine the racial identity, discuss the former status, and document the current distribution and abundance of Water Pipits breeding in the mountains of California. We also discuss hypotheses regarding the dynamics of colonization.

STUDY AREAS AND METHODS

Alpine habitat in California occurs in the Klamath, Cascade, Sierra Nevada, Sweetwater, and White Mountain ranges (Major and Taylor 1977) (Fig. 1). The vast majority of alpine area in the states is found in the Sierra Nevada, stretching from Olancha Peak (Tulare County, 36°16′N) in the south, north to the Lake Tahoe vicinity (El Dorado County, 38°50′N). The alpine zone occurs at elevations above approximately 3,350 m in the southern Sierra, dropping to 3,050 m in the northern part of the range. The largest expanses of alpine vegetation in the Sierra Nevada are found in a nearly continuous band of roughly 3,000 km^2 from the Great Western Divide and Sierra Crest in the south to slightly north of Sonora Pass in the north, a distance of some 260 km (Fig. 1). Additionally, the Warner Mountains in northeastern California (Modoc County) and San Gorgonio Mountain in southern California (San Bernardino County) include subalpine summits which harbor small enclaves of relict alpine vegetation.

We investigated the historical status of Water Pipits in California by searching published literature and unpublished field notes at the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), and the Yosemite National Park Natural History Museum (YNPNHM). We also compiled published and unpublished records of recent pipit sightings in the state.

We conducted fieldwork for this study from 1982 through 1986; most of our distributional, breeding density, and racial data were collected between late May and early August in 1984 and 1985. We attempted to determine the current breeding distribution of Water Pipits in California by surveying nearly every alpine region in the state, as well as the two subalpine areas mentioned above. Distribution surveys consisted of walking through appropriate alpine habitat searching for pipits and recording habitat data (availability of mesic tundra vegetation, riparian areas, and snowbanks). In each region we attempted to cover as much optimal habitat as possible in 1 or 2 days.

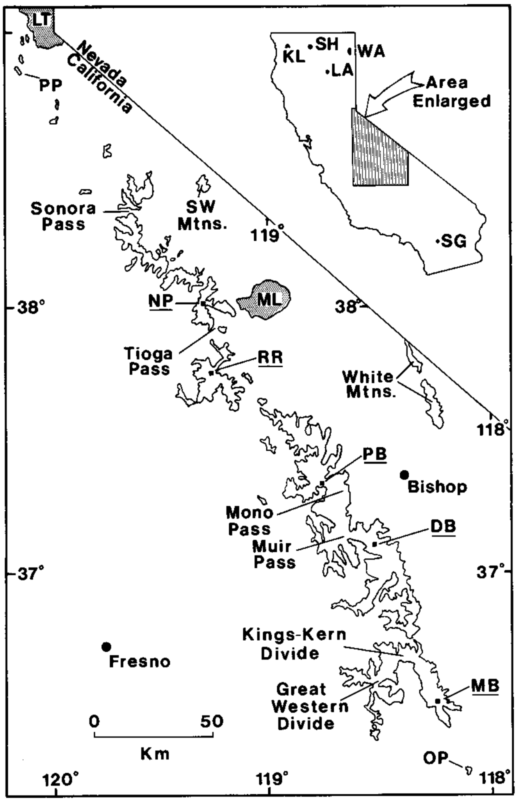

FIGURE 1. Map of alpine regions of the Sierra Nevada, White, and Sweetwater (SW) Mountains, California (redrawn from Kuchler 1977). Census plots (MB, DB, PB, RR, NP) are described in text and in Table 1. Lake Tahoe (LT), Mono Lake (ML), and the cities of Fresno and Bishop are included as reference points. OP = Olancha Peak, PP = Pyramid Peak. Inset shows location of map and additional pertinent areas: Klamath Mountains (KL), Mt. Shasta (SH) and Mt. Lassen (LA) (Cascade Range), Warner Mountains (WA), and San Gorgonio Mountain (SG).

Within the Sierra Nevada we made over 25 trips during which we searched for pipits in most large expanses of alpine habitat throughout the range. We devoted extra attention to areas which marked the apparent limits of this species' distribution.

We searched the following non-Sierran areas between 20 May and 20 July 1984: Eagle Peak, Warner Mountains (Modoc County); Panther Creek and other western drainages on Mts. Shasta and Shastina (twice) (Siskiyou County) and Mt. Lassen (twice) (Shasta County), Cascade

TABLE 1. Water Pipit census areas and census results in the Sierra Nevada, California.

Census area	Coordinates	Elevation (m)	Total plot area (ha)	Mesic area in plot (ha)	% mesic area in plot	No. of pipits[a]	Density (birds/ha mesic)	No. of nests[b]
Mitre Basin (MB)	36°32′N 118°16′W	3,410–3,660	146	18	12	34	1.89	12
Dusy Basin (DB)	37°06′N 118°32′W	3,440–3,600	120	17	14	21	1.24	8
Pioneer Basin (PB)	37°28′N 118°48′W	3,290–3,540	383	33	9	0	0.00	0
Ritter Range (RR)	37°43′N 119°11′W	2,990–3,350	139	50	36	5	0.10[c]	0
North Peak (NP)	37°59′N 119°18′W	3,170–3,410	160	22	14	15	0.68	4

[a] Includes nesting pairs and unmated territorial males within census plot boundaries during census periods.
[b] Includes only pipit nests located within census plot boundaries.
[c] Not strictly comparable to other density values. See text for explanation.

Mountains; Mt. Patterson vicinity, Sweetwater Mountains (Mono County); White Mountain Peak vicinity, White Mountains (Mono County); San Gorgonio Mountain (San Bernardino County); and San Jacinto Mountain (Riverside County). We visited San Gorgonio Mountain again in 1985. We did not visit the Klamath Mountains, where alpine communities are very limited (Major and Taylor 1977).

In 1985 we measured breeding densities of Water Pipits in five alpine locations (Fig. 1) at roughly equidistant intervals along the known pipit breeding range in the Sierra Nevada. All census areas were located at or above tree limit and were selected to be representative of local suitable habitat. Location, size, and additional details of these census plots are given in Table 1.

In the Mitre Basin (MB), Dusy Basin (DB), and North Peak (NP) census areas we surveyed the available habitat and selected census plots to include as much optimal moist and wet alpine meadow as was possible for two persons to walk through slowly during a 3–5-hr census period. We attempted to standardize the approximate area of mesic habitat included in each census plot, rather than the total plot size. Each author performed four to six censuses per location in MB, DB, and NP, with approximately equal numbers in the morning and evening. Census periods averaged 4 hr in length, and were conducted during 4- or 5-day periods in each area. Because pipit densities were very low in the Ritter Range (RR) and Pioneer Basin (PB) census areas, we censused larger areas less intensively. Miller censused the RR plot for four periods ($\bar{x}$ = 3.2 hr) over 3 days. Green searched for pipits for 15.5 hr over two 2-day periods in PB. In both of these regions additional time spent searching adjacent areas corroborated the densities found in the plots.

Censusing involved mapping the location of all pipit sightings on enlarged (4×) USGS 15′ topographic maps. The approximate distribution of wet and moist tundra vegetation (mesic tundra) in each plot was mapped by visual inspection. We concentrated our census efforts on wet and moist meadows, as these are preferred nesting and foraging habitats, but all area within plots was thoroughly covered. Pipit density values (birds/hectare mesic tundra habitat in census plots) include breeding pairs with known nests in the plots, and pairs or individual singing males whose mapped activities were centered in the census plot and appeared to have territories within the plot boundaries. Thus, the densities reported here are uniformly conservative, as sightings not assignable to known territories were deleted (except in the RR census area, as discussed in results).

On each day that we performed censuses we also spent roughly equal periods (ca. 4 hr/person/day) observing known pairs to locate their cryptic nests. We trapped adults with a drop net erected over the nest. These nets were constructed from a 1-m^2 piece of mist net with curtain weight tape sewn around the border and supported by a PVC pipe frame. Nets were operated from up to 150 m away by a monofilament pullcord.

We measured, banded, and took in-hand photographs of the captured birds. Full-frame ventral and lateral shots were taken of each bird juxtaposed with a color reference scale and an identification number. Exposures were adjusted by using an 18% gray card oriented perpendicular to the sun. We used Kodacolor color print film (ASA 100) and had 8.9 × 12.7 cm glossy prints made by a custom lab. Photographs effectively recorded the extent of ventral streaking. Although the fidelity of color reproduction was not excellent, it was nonetheless possible to distinguish between a designated three-level scale of ventral color saturation (see below) in nearly all photographs.

We collected one female and four male pipits between 25 May and 15 July from five locations throughout their present range in the Sierra. These specimens are housed at MVZ (Nos. 169896, 97, 98) and the American Museum of Natural History (Nos. 817196, 97). Subsequently, R. E. Johnson collected an additional female and immature (Charles R. Connor Museum).

For our racial analysis we used the following museum specimen samples (collected between 20 May and 31 July on breeding grounds): 32 male and 13 female *alticola* from Montana, Wyoming, and Colorado; 26 male and nine female *pacificus* from Washington and British Columbia (Coastal Ranges); 15 males and 16 females from the Wallowa Mountains of Oregon which were classified as *pacificus,* but which we treated as a distinct group because they appeared to be intermediate between these two races; and 18 males and 21 females from the Sierra Nevada (of these, 14 males and 19 females represent measurements and photographs of live birds). Measurements used in this analysis included: unflattened wing chord, tail length (base of central rectrices to tip of longest rectrix), bill length (anterior edge of nares to tip), and hind claw chord.

All specimens were scored for breast color and extent of ventral streaking. Specimens were randomly arrayed with only the breast and throat exposed and compared with five specimens (*pacificus* and *alticola*) selected to form a uniform scale of streaking. For color analysis we classified specimens as more (3), equally (2), or less (1) saturated with orange pigments than one reference specimen (*pacificus*) of intermediate value. Both authors independently scored each bird and disagreements (ca. 10%) were settled by discussion. All color comparisons were made under a MacBeth Super Color-Matching Skylight (Model BX 848A). Photographs of Sierran birds were scored in a similar fashion.

RESULTS

RACIAL IDENTITY

Anthus s. alticola averages larger (wing and tail length) and, in alternate plumage, is considerably more richly colored and less heavily streaked ventrally than *pacificus* (Ridgeway 1904, Todd 1939, Phillips et al. 1964). Sierran pipits are similar to Rocky Mountain specimens in both color and mensural characters of both sexes. In comparisons of males, four characters (wing chord, tail length, ventral color, and ventral streaking) differed significantly between Sierran and Cascade birds, but not between Sierran and Rocky Mountain birds (Table 2 and Fig. 2). Bill and hind claw lengths showed considerable variation and weakly supported (hindclaw) or contradicted (bill) the Sierra-Rocky Mountain affinity.

Comparisons of females followed a similar trend: Sierran birds differed from Cascade birds in all characters, but differed from Rocky Mountain birds only in wing chord length (Table 3). Within each population, females averaged smaller, duller, and more heavily streaked than males.

Specimens from the Wallowa mountains of eastern Oregon were formerly considered to be *pacificus.* However, our results show that they are intermediate between *pacificus* and *alticola* in size, color, and streaking. Sierran pipits do not show similar evidence of intergradation.

HISTORICAL OCCURRENCE

Historical records of Water Pipits during the breeding season (May to August) in California are very scarce prior to 1970. Merriam (1899: 130) heard pipits displaying on 17 July on Mount Shasta in northern California, although Miller (1939) did not find pipits or suitable breeding habitat there. Ridgeway (1904) stated that pipits bred in the Sierra Nevada, but did not provide supportive evidence, as he did for other locations; his inclusion of the Sierra in this species' breeding range may have been speculative. A single pipit was found on 1 July on Mt. Lassen, three east of Mt. Lassen (Silver Lake) on 1 August (Vogt 1941), and twelve pipits were seen on 24 August at Piute Pass, Fresno County (Cogswell

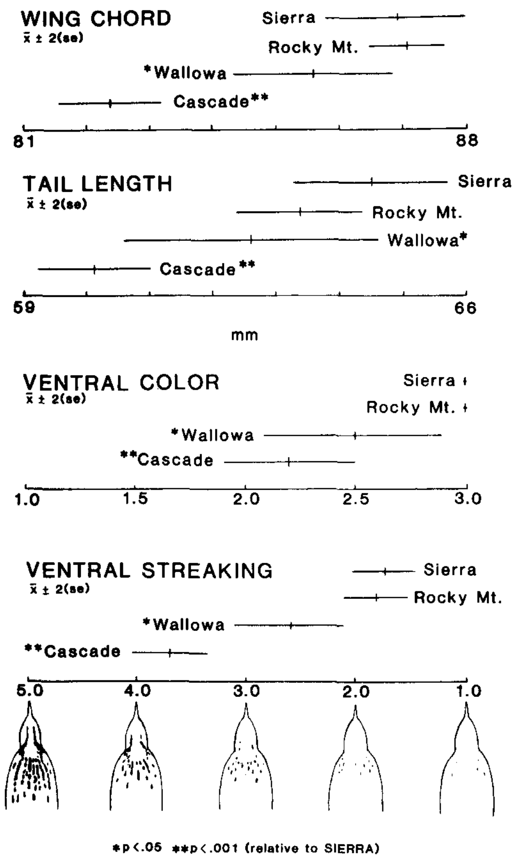

FIGURE 2. Comparison of four principal characters used to determine racial identity of Sierran Water Pipits. Data are from males. Measurements and sample sizes are given in text and in Table 2.

TABLE 2. Comparison of measurements and plumage of male Water Pipits from the Sierra Nevada (SN), Rocky Mountains (RM), Wallowa Mountains (WA), and Cascade/North Coast ranges (CR).[a]

Character	Source	$\bar{x} \pm 2$ (SE)[b]	n	CV[c]
Wing chord	SN	86.9 ± 1.1	17	2.7
	RM	87.1 ± 0.6	31	1.9
	WA	85.6 ± 1.2*	16	2.8
	CR	82.4 ± 0.8***	24	2.4
Tail length	SN	64.5 ± 1.2	17	3.8
	RM	63.4 ± 1.0	31	4.2
	WA	62.6 ± 2.0*	15	6.5
	CR	60.1 ± 0.9***	26	3.8
Bill length	SN	9.6 ± 0.2	18	5.0
	RM	10.0 ± 0.2*	32	4.3
	WA	9.5 ± 0.2	16	3.5
	CR	9.4 ± 0.2	20	5.5
Hind claw length	SN	7.3 ± 0.3	16	8.2
	RM	8.1 ± 0.4*	32	14.9
	WA	7.5 ± 0.5	16	12.6
	CR	8.7 ± 0.4**	26	12.9
Ventral streaking	SN	1.7 ± 0.3	15	34.2
	RM	1.8 ± 0.3	26	44.3
	WA	2.6 ± 0.5†	14	36.5
	CR	3.7 ± 0.4††	23	23.7
Ventral color	SN	3.0 ± 0.0	15	0.0
	RM	3.0 ± 0.0	26	0.0
	WA	2.5 ± 0.4†	16	32.7
	CR	2.2 ± 0.3††	24	32.6

[a] The origin of samples is given in text.
[b] Probability levels are relative to Sierra Nevada sample.
[c] Coefficient of variation.
* $P < 0.05$, ** $P < 0.005$, *** $P < 0.001$, Student's t-test.
† $P < 0.01$, †† $P < 0.0001$, Mann-Whitney U-test.

1956). High elevation records from the fall (September to October) are only slightly more common, including several sightings on and near Mt. Lassen (Vogt 1941), two in a subalpine meadow on the Warren Fork of Lee Vining Creek, Mono County (J. Grinnell, unpubl. notes, 1915, MVZ); two at Helen Lake, Tuolomne County (C. and E. Michaels, unpubl. notes, 1926, YNPNHM); several records at and above the treeline in the Mt. Lyell vicinity, Tuolomne County (Harwell 1933, unpubl. notes, 1943, YNPNHM); and a sighting in subalpine Horse Corral Meadow, Fresno County (Dixon 1943).

More striking than these few records is the absence of sightings by the many ornithologists and naturalists who spent time in alpine habitat in the Sierra. We have examined records of a number of early collecting trips and naturalist excursions to places where pipits now breed, but from where they were not previously reported. A partial list of these locations includes: Kuna Crest and Mt. Lyell vicinity (C. Michaels, unpubl. notes, 1922, 1925, YNPNHM); Muir Pass, Evolution Lake Valley, and Darwin Canyon and Creek (Dixon 1943); Rocky Basin Lakes, Cottonwood Lakes, Siberian Outpost, and the Kuna Crest vicinity (Grinnell, unpubl. notes, 1911, MVZ); and Piute Pass and Humphreys basin (W. C. Russell, unpubl. notes, 1954, MVZ). Dawson (1923) also spent considerable time in the Sierran alpine, including the Cottonwood Lakes Basin, without detecting Water Pipits. Grinnell (1908, unpubl. notes, 1911 MVZ) visited the summit of San Gorgonio Mountain more than six times between 1905 and 1907 without finding pipits there.

The first breeding season records for the Sierra include one record from 1971 at Saddlebag Lake, Mono County (DeSante and LeValley 1971:904) and two records from 1972 in the Evolution region, Fresno County (DeSante and Remsen 1972: 903). In 1975 two widely separated nests were found in Mono and Tulare Counties (Stallcup and Winter 1975:1028, Norris and Morgansen 1982), and since that time numerous sightings and occasional nests have been reported from various parts of the southern and central Sierra (D. DeSante, D. Gaines, H. Green, L. Norris, and others, pers. comm.). In 1978 a pair of pipits was found nesting near the summit of San Gorgonio Mountain (McCaskie 1978).

TABLE 3. Comparison of measurements and plumage of female Water Pipits from the Sierra Nevada (SN), Rocky Mountains (RM), Wallowa Mountains (WA), and Cascade/North Coast ranges (CR).[a]

Character	Source	$\bar{x} \pm 2$ (SE)[b]	n	CV[c]
Wing chord	SN	80.5 ± 0.8	20	2.2
	RM	82.1 ± 1.5*	13	3.2
	WA	79.3 ± 0.8	15	1.9
	CR	77.4 ± 0.8*	8	1.4
Tail length	SN	59.9 ± 1.4	19	5.2
	RM	59.1 ± 1.3	12	3.8
	WA	59.1 ± 1.5	16	5.2
	CR	56.8 ± 1.5*	9	3.9
Bill length	SN	9.7 ± 0.2	21	4.0
	RM	9.8 ± 0.2	12	3.7
	WA	9.3 ± 0.2*	15	4.5
	CR	9.2 ± 0.2*	10	3.0
Hind claw length	SN	8.3 ± 0.4	17	10.8
	RM	8.9 ± 0.5	13	9.2
	WA	7.8 ± 0.5	16	11.8
	CR	9.5 ± 0.8**	10	13.3
Ventral streaking	SN	2.7 ± 0.3	17	25.3
	RM	2.7 ± 0.5	8	25.7
	WA	3.1 ± 0.4	14	24.5
	CR	4.5 ± 0.5††	6	12.2
Ventral color	SN	3.0 ± 0.0	11	0.0
	RM	2.9 ± 0.3	8	12.3
	WA	2.7 ± 0.3†	14	17.3
	CR	2.3 ± 0.6†	7	33.1

[a] The origin of samples is given in text.
[b] Probability levels are relative to Sierra Nevada sample.
[c] Coefficient of variation.
* $P < 0.05$, ** $P < 0.005$, Student's t-test.
† $P < 0.01$, †† $P < 0.0001$, Mann-Whitney U-test.

CURRENT DISTRIBUTION AND ABUNDANCE

We did not find pipits in the Cascade (Mts. Shasta and Lassen), Sweetwater, White, or Warner Mountains. We found approximately five pipit pairs maintaining territories near the arid summit of San Gorgonio Mountain in both 1984 and 1985.

In the Sierra Nevada we found Water Pipits during the breeding season as far north as Tower Peak (38°08′, Mono County) and as far south as Franklin Lakes (36°25′, Tulare County) and Rocky Basin Lakes (36°27′ Tulare County) along the Great Western Divide and Sierra Crest, respectively. We heard a single pipit in late August 1985 near Pyramid Peak (El Dorado County), however this northern record may have been a fall migrant; we found no pipits in this location in June 1984.

The southern limit of pipit breeding in the Sierra Nevada coincides approximately with the southern boundary of mesic alpine habitat; the southernmost nesting record is from Cottonwood Lakes Basin, and nesting is probable in the Rocky Basin Lakes, 5 km to the southwest. The northernmost nesting location we found is in the North Peak census area. Ryser (1985), however, reports a nest from Mount Rose in the vicinity of Lake Tahoe (Washoe County, Nevada) much farther north. Although densities were moderately high in the North Peak area, we made only two sightings of individual pipits north of the NP census area, despite many days of searching in 1984 and 1985.

Densities were highest in the MB census area at 1.9 birds/ha of mesic meadow, declining to 1.2 birds/ha mesic meadow in the DB area (Table 1). Densities were lowest in PB, where no pipits were sighted in 15.5 hr, and in RR where only five birds were sighted in 13 hr. The density of 0.1 bird/ha mesic meadow in RR shown in Table 1 probably overestimates the actual breeding density because the only confirmed breeding pair in this area may have nested outside of the census plot, and it was not possible to locate the territories of the other (briefly) observed pipits. Densities were moderately high in the NP area (0.7 bird/ha mesic meadow).

Our census results are corroborated by the frequency of sightings made in regions adjacent to and between the census areas. Within their current limits of distribution, pipit abundance was neither uniform nor continuous. Densities were highest in the southern part of the range, especially in the vicinity of the Sierra Nevada Crest and Kings-Kern Divide. Between the Kings-Kern Divide and Mono Pass distribution is fairly continuous in areas of optimal habitat, although abundance varies noticeably in apparently comparable areas. Between Mono Pass and the NP census area distribution becomes markedly patchy: areas of moderately high abundance are separated by large areas where pipits are uncommon or absent. North of the NP census area pipits are rare.

DISCUSSION

The significant differences in size and pronounced differences in color and streaking between Sierran Water Pipits and *pacificus,* and the high degree of similarity between Sierran birds and *alticola* indicates that the California breeding population derives from the Rocky Mountains or Great Basin Ranges and should be classified as *alticola.*

We found that differences in alternate plumage between these two western pipit races are not a result of wear or fading. Following the postnuptial molt (August to September) both races are heavily streaked and quite similar in appearance. A partial prenuptial molt (March to April) results in distinctive breeding plumages: *alticola* becomes sparsely streaked or unstreaked, and richly orange-rust colored ventrally, whereas *pacificus* molts into an equally heavily streaked and somewhat paler plumage. Williamson (1965) described in detail parallel differences in molt and plumage between European races of *A. spinoletta.*

Intermediate size and plumage observed in the Wallowa Mountains population appears to be the result of intergradation between *pacificus* and *alticola.* This is not surprising in consideration of the geographic proximity and ecological affinities of the Wallowa Mountains to both Cascade and Rocky Mountains of similar latitude.

While it is not possible to determine with certainty the historical status of Water Pipits in California, we believe it is very unlikely that they were present at current densities and were simply overlooked. The Sierran alpine was not neglected by naturalists and was, in fact, among the most frequently visited and well known alpine regions in America. By way of comparison, by the 1950s pipits were known to breed in the Olympic Mountains of Washington (Kitchin 1949), Wallowa Mountains of Oregon (Gabrielson and Jewett 1940), Bitterroot Mountains of Idaho (Burleigh 1972), Uinta Mountains of Utah (Hayward 1952), Rocky Mountains of Colorado (Bailey and Niedrach 1965), San Francisco Peaks of Arizona (Phillips et al. 1964), and the mountains of north-central New Mexico (Bailey 1928). They were also known to breed in the following National Parks: Mt. McKinley, Alaska; Glacier, Montana; Mt. Rainier, Washington; Grand Teton and Yellowstone, Wyoming (Checklist of the Birds of National Parks 1939). Yet for the Sierra Nevada, which contains three of the largest parks in the west and was comparatively well-explored, Water Pipits were virtually unknown during the breeding season, and seldom sighted during fall migration (Beatty et al. 1933, Grinnell and Miller 1944, Summer and Dixon 1953).

The status of the few historical Sierran sightings in September and October and the single record from Piute Pass in late August is problematic. These birds may have been local breeders, or may have been migratory *pacificus* which typically begin to appear in lowland and mid-elevation locations in California during September. Likewise, the status of summer and fall records from northern California on Mts. Shasta and Lassen is questionable. Gabrielson and Jewett (1940) reported migratory pipits, almost certainly *pacificus,* from alpine and subalpine elevations in the Oregon Cascades, and we have observed flocks of migratory *alticola* above and at tree limit in the Rocky Mountains. Thus, Water Pipits do at times migrate through high montane regions. It remains to be determined, however, if *pacificus* occasionally passes through the Sierran alpine.

It is possible that pipits have nested sporadically and sparsely in the Sierra Nevada and Cascade volcanoes throughout historical times. However, the paucity of historical breeding season records, the absence of pipits 30 or more years ago from specific locations where they are now fairly common, and the many records since the early 1970s, when taken together, strongly suggest that a recent and rapid colonization and/or major demographic expansion has occurred over the last several decades or less.

The absence of breeding Water Pipits from alpine regions outside of the Sierra Nevada is not surprising. The arid volcanic soils of Mts. Shasta and Lassen support limited and depauperate alpine vegetation, and the Sweetwater and White Mountains are arid Great Basin ranges which also do not contain much mesic tundra. Neither the Warner Mountains nor San Gorgonio Mountain supported habitat we considered suitable for breeding Water Pipits. The small pipit population persisting on the summit and upper north slope of San Gorgonio occupied very arid, sparsely vegetated talus and sand slopes. This is the most xeric and atypical breeding location we have seen and suggests that, eventually, small populations may nest in other arid ranges of California, as well.

The regional pattern of Water Pipit distribution and abundance in the Sierra Nevada does not seem to reflect the overall availability of their preferred breeding habitat in this range. During the nesting season Water Pipits are typically associated with moist or wet alpine sod-forming vegetation. Of 45 nests we found in the Sierra Nevada, 30 were located in mesic tundra and the remainder occurred within a short distance of this favored foraging habitat. Mesic tundra is most abundant in parts of the central Sierra Nevada (Muir Pass to Sonora Pass, Fig. 1). In the arid southern part of the range mesic communities tend to be limited in extent and restricted to riparian locations, while north of Sonora Pass alpine habitat occurs on isolated summits and ridges, which support very little mesic tundra.

Pipit distribution is patchy in the Sierra Nevada, even in their preferred habitat. On a regional scale, however, densities are highest, distribution is most uniform, and the population is largest in the southern part of the range. This pattern of abundance is not readily explainable in terms of habitat considerations. Instead, it suggests that pipits first became established in the southern Sierra Nevada and are expanding northward. The absence or scarcity of pipits in areas of excellent breeding habitat in the north-central part of the Sierra Nevada lends additional support to this interpretation. If our hypotheses regarding recent colonization and expansion are correct, we predict an extension of the northern breeding limit and an increase in breeding density in the central and northern parts of this species' range over the next decade.

The dynamics of the apparently rapid establishment of Water Pipits in the Sierra Nevada is puzzling. Why were they absent or rare in this major mountain range until recent times, and why has *alticola* become established, instead of the locally common *pacificus*? We speculate that the previous absence of a vigorous Water Pipit population in the Sierra Nevada may be attributable to, and date from, the latest paleoclimatic warming episode which eliminated suitable breeding habitat from the range. Earlier Pleistocene climatic changes were probably responsible for isolation and differentiation of the three North American Water Pipit races, a fact we believe to be of importance in understanding their current distributions.

Arctic and alpine tundra ecosystems and their biota have been greatly influenced by repeated cycles of climatic cooling and warming during and since the Pleistocene. Extremes of both glacial and warmer interglacial periods restricted the size and extent of alpine tundra regions, thereby isolating or causing extinction of certain populations; these effects were enhanced by the insular nature of alpine regions. Present distributions of certain avian taxa, especially tundra forms, reflect genetic isolation during glacial and xerothermic periods (Rand 1948, Hoffmann and Taber 1967, Johnson 1972); the three North American Water Pipit races apparently exemplify this type of origin. *Anthus s. rubescens* was isolated in the central or eastern Canadian arctic or Greenland; *pacificus* persisted in the arctic tundra of Alaska, but also expanded southward through the coastal ranges as conditions permitted; and the range of *alticola* migrated along the Rocky Mountain cordillera in response to alpine tundra movements.

Since the recession of the last Wisconsin glaciers (ca. 10,000 years ago) periods of cooler than present climate resulted in larger, more widespread alpine regions and facilitated biotic exchange among western mountain ranges (Billings 1978, Brown 1978). At such times Water Pipits and other widespread alpine taxa such as the White-tailed Ptarmigan (*Lagopus leucurus*) probably inhabited the Sierra Nevada. Subsequently, a strong temperature maximum, the Hypsithermal, lasting from approximately 5,000 to 2,900 years ago (LaMarche and Mooney 1957, Adam 1967), depleted alpine plant and animal communities throughout western North America (Hoffmann and Taber 1967, Chabot and Billings 1972, Billings 1978). The Sierra Nevada and other southern ranges which lack orographic continuity with the major cordillera were especially affected, because conditions here were most xeric and because certain mesophytic plants and associated animals which vanished during the Hypsithermal have not yet recolonized these areas. Water Pipits probably became extinct in the Sierra Nevada as mesic tundra disappeared during the Hypsithermal.

Why did pipits of either western race fail to recolonize the Sierra long ago as appropriate habitat became available? We suggest that habitat and climate differences between its northern breeding grounds and the California ranges have prevented *pacificus* from becoming established in the state, and that the Great Basin provided an effective dispersal barrier which hindered colonization by *alticola.*

Anthus s. pacificus evolved in arctic and northern alpine tundra environments which are relatively low in elevation, moist, and cloudy. Tree limit occurs at 2,000 m in the Washington Cascades, near the southern limit of the breeding range of *pacificus,* and drops to sea level in arctic Alaska. In comparison, tree limit occurs at 3,350 m in the southern Sierra Nevada and at 3,500 m in the Colorado Rockies. Relative humidity is higher and potential evapotranspiration lower in the coastal ranges than in either the Sierra or the Rockies (Major and Bamberg 1967, Olmsted 1976), and total plant coverage, especially the coverage of mesic communities, is lower in the Sierran alpine than in either the coastal ranges or the Rockies (Hayward 1952, Chabot and Billings 1972, Douglas and Bliss 1977, Billings 1978).

Temperature and humidity extremes have been shown to be physiologically important in habitat segregation by congeneric bird species (e.g., Salt 1952), and might also affect widely separated races in a similar fashion. For *pacificus,* geographic barriers cannot be invoked as explanation for their absence from the Sierra: each year this race has ample opportunity to invade the Sierra but has failed to colonize successfully. The high elevation and xeric nature of the Sierran alpine is a likely cause for this absence.

Although the Rocky Mountains receive considerably more summer precipitation and cloudiness than the Sierra Nevada (Baker 1955), the alpine zone in these interior ranges occurs at similarly high elevations as in the Sierra. In terms of climate and visual characteristics, much greater similarity exists between the Sierra and southern Rockies than between either of these ranges and the north coast ranges. Some southern Rocky Mountain *alticola* populations, as well as those of certain Great Basin ranges, breed in fairly arid habitats which might preadapt these individuals to Sierran conditions.

The Great Basin desert has provided dispersal barriers for several alpine and boreal avian taxa (Behle 1978). Likewise, the prior absence or scarcity of *alticola* in the Sierra Nevada seems to be most readily explained by the large distance between California and this taxon's "normal" range. The timing of colonization of the Sierra Nevada may have been fortuitous, a result of stochastic dispersal of individuals from the Rocky Mountains. Alternatively, prior establishment of small populations in the Great Basin ranges may have facilitated eventual colonization by serving as intermediate sources of dispersers in both space and time.

ACKNOWLEDGMENTS

We thank Ned K. Johnson for assistance and for use of the Museum of Vertebrate Zoology collections, and Richard E. Johnson for valuable discussions and for providing additional specimens. Supplemental distribution information was supplied by David DeSante, David Gaines, Helen Green, and Larry L. Norris. Racial comparisons were made possible by loans from the following museums: British Columbia Provincial Museum, Charles R. Connor Museum (Washington State University), Denver Museum of Natural History, San Diego Museum of Natural History, United States National Museum, University of British Columbia, and the University of Puget Sound. We are grateful to the following persons for critical review of the manuscript at various stages: Daniel Airola, David DeSante, Ned K. Johnson, Richard E. Johnson, Helmut C. Mueller, Larry L. Norris, David Shuford, David F. Westneat, R. Haven Wiley, and David Winkler. In 1985 our fieldwork was partially funded by a Frank M. Chapman grant from the American Museum of Natural History. We are especially indebted to Helen Green for assistance throughout the study.

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