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HABITS AND HABITATS OF MOUNTAIN PLOVERS IN CALIFORNIA[1]

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Abstract. Continental populations of the Mountain Plover (*Charadrius montanus*) have declined drastically in the last quarter century. Despite many investigations of its breeding biology, the species has never been studied during the winter. Historically, most birds have wintered at lower elevations in inland California. We used radio telemetry to describe the movement patterns and habitats of plovers on the Pixley National Wildlife Refuge, Tulare County (1992–1993) and Carrizo Plain, San Luis Obispo County (1993–1994) of California. The first plovers were seen 7–20 October each year, with most birds arriving in early November. The daily survival rate for the 44 transmittered plovers was 0.9996 based upon 2,395 telemetry days of information. The calculated survival probability for the 1 November to 15 March winter period was 0.9474. Plovers foraged and roosted in loose flocks of 2 to >1,100 birds, with average flock size increasing late in the season at premigratory staging areas. Flock integrity was poorly developed as birds captured and telemetered together were, with one exception, not relocated together. The average minimum distance that the 44 plovers moved was 1.17 ± 1.42 km/day. Movements of individuals were highly variable due to the tendency of a bird to remain at a locale for a few days then move to a new area. Plovers moved >55 km between weekly relocations on seven occasions. The longest documented move was 127 km across the Temblor Mountains between 29 December 1993 and 5 January 1994. Site fidelity seemed poorly developed and the Carrizo Plain and southern San Joaquin Valley populations were considered biologically sympatric.

Plovers at the Pixley NWR were usually relocated on contiguous croplands that had been recently cultivated. At both study areas, however, plovers preferred heavily grazed native rangelands. They used burned fields primarily for night roosting. Alkali flats, historically extensive but virtually nonexistent today, were the most favored habitat, where available. Flocks of plovers departed from California in mid-March each year and were recorded back on breeding areas in Colorado the third week of March. We conclude that plovers are being forced to use cultivated lands during winter in the San Joaquin Valley, and birds in relict populations at both locales are dependent upon core areas of native habitat in October and November especially.

Key words: *Mountain Plover;* Charadrius montanus; *movements; habitats; San Joaquin Valley, California.*

INTRODUCTION

The Mountain Plover (*Charadrius montanus*) is one of 12 bird species endemic to the North American grasslands (Mengel 1970). Data from the annual Breeding Bird Survey indicate that continental populations of over half of those 12 species declined from 1966–1991 (Knopf 1994), with Mountain Plovers declining at an annual rate of 3.7% ($P < 0.01$) through 1993. The declines in this plover population may represent a continuation of a longer term process as seen in the historical contraction of the continental breeding range of this species (Graul and Webster 1976).

Mountain Plovers breed on the western Great Plains and in contiguous arid, or disturbed, landscapes. Nests are generally located in areas of very short vegetation, sometimes among scattered shrubs, and also on bare ground (Graul 1975, Shackford 1991, Knopf and Miller 1994). Despite the extensive fragmentation of the western Great Plains by agriculture, reproductive success of plovers appears stable in native habitats (Miller and Knopf 1993).

Historically, the Mountain Plover wintered from southern Texas and northern Mexico westward to the Pacific Coast. Plovers apparently have always been irregular visitors during the winter in Texas (Oberholser 1974), and the largest concentrations have been in the Central Valley of California (Fig. 1). This paper reports on the movements, flocking behavior, and habitat use

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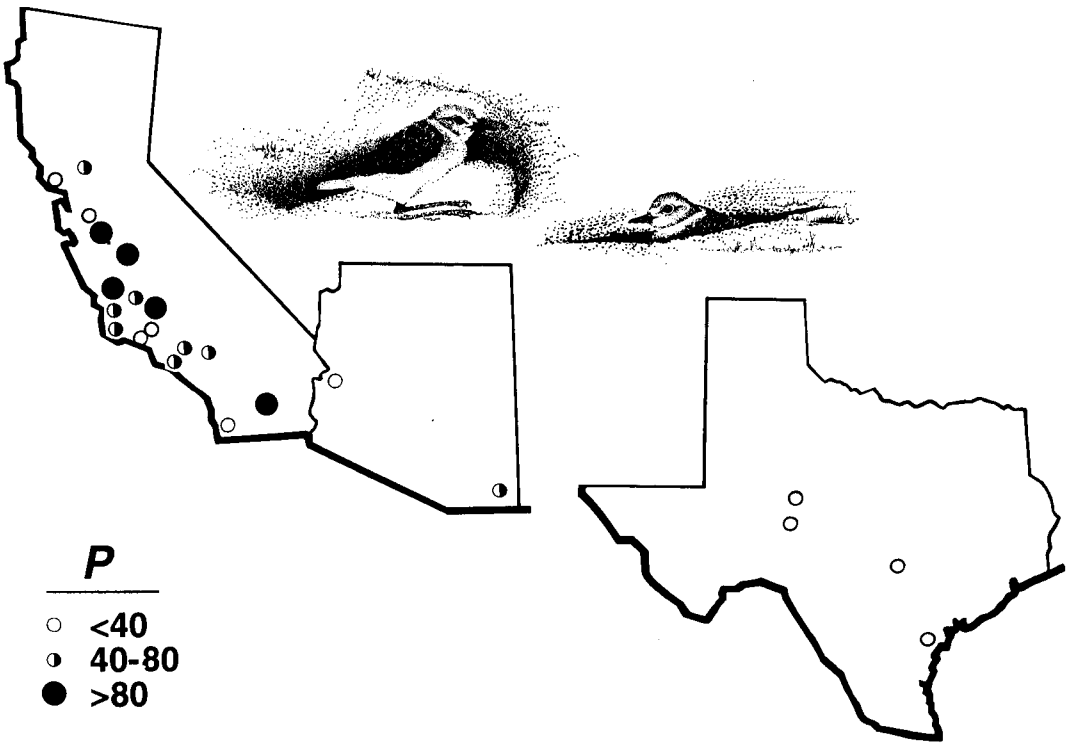

FIGURE 1. Wintering distribution of Mountain Plovers based upon Christmas Bird Count data, 1959–1992. Plotted symbols identify areas based upon their probability of use by plovers across the 34 years. Counts that only recorded Mountain Plovers once were considered accidentals and not included. The five California count locales with greatest predictability of plovers appearing in a given year are Carrizo Plain, Creighton Ranch, Lancaster, Panoche Valley, and Salton Sea South. Drawings illustrate the tendency of wintering Mountain Plovers to roost in shallow depressions. Birds rest on the tarsus at a depth such that the eye is just visible above the surface.

of birds in California and represents the first study of the species during the wintering period.

STUDY AREA

We studied Mountain Plovers at two locales in southern California in the winters of 1992–1993 and 1993–1994. The first season we concentrated studies at the Pixley National Wildlife Refuge (NWR), Tulare County. The second season we worked on the Carrizo Plain, San Luis Obispo County. The study areas are at 70 m and 550–680 m elevation, respectively, approximately 100 km apart, and are separated by the Temblor Mountains which rise to 1,160 m.

The natural vegetation of the San Joaquin Valley was recently described and mapped relative to endangered species of the region (Anderson et al. 1991). Only 2.9% of the San Joaquin Valley floor where Mountain Plovers spend the winter remains in good-or-better natural condition. Of the four natural vegetation community types, Mountain Plovers use the Valley Sink Scrub type and Non-native Grassland type. The former occurs in low areas of heavy, saline or alkaline clays of historical lakebeds (Buena Vista, Goose, Kern, Tulare) north along the trough of the San Joaquin Valley through Merced County to the grasslands of the Sacramento Valley. Vegetation is dominated by alkali-tolerant Chenopodiaceae, especially *Allenrolfea occidentalis* and several *Sueda* species. The Non-native Grasslands occur on fine-textured, mostly clay soils that become waterlogged or inundated during the winter rainy season and dry out completely in summer. Grasslands historically covered valleys and foothills of most of California. Current vegetation is annual grasses of 0.2–1.0 m height with inter-

mixings of annual forbs. The native vegetation types not used are Valley Saltbush Scrub and Interior Coast Range Saltbush Scrub, both of which occur on sandy to loamy, non-alkaline soils.

The Carrizo Plain is drier than the San Joaquin Valley. The year prior to our studies this area had not received rain for three years and was unvegetated bare ground. The plain has clay and alkaline soils similar to those where Mountain Plovers are found in the valley and vegetation associations also appear similar.

METHODS

Beginning in late October, Mountain Plovers were located at dusk and watched until dark on clear, moonless, fog-free nights. After a wait of several hours, we located the birds by spotlighting with a 1×10^6-candlepower, backpack lamp. Plovers were generally detectable at 80–100 m using binoculars. Mountain Plover eye shine was distinguished as single reflections from a group of stationary, inactive points, which was in contrast to the highly active paired-eye reflections from nocturnal rodents and spiders. Birds were generally spaced up to 15 m apart. We approached within 2 m of a plover and used either a long-handled net or a netted throw-ring (1-m diameter) to capture the bird. Once a few birds were transmittered, we relocated them after dark on clear nights and captured additional birds roosting with them.

Netted birds either flushed into the net and were quickly restrained or merely sat still until picked up. Plovers remained calm during handling. We banded each bird with a U.S. Fish and Wildlife Service band and colored plastic bands to facilitate confirmation in resightings. A 2.7–3.0 g radio transmitter with a 15 cm antenna (Holohil Ltd., Woodlawn, Ontario, Canada, and Advanced Telemetry Systems, Inc. Isanti, Minnesota. Mention of commercial products does not constitute endorsement by the U.S. Government) was affixed by applying a light coating of waterproof adhesive (Titan Corp., Lynnwood, Washington) to the transmitter and placing it under the upper back feathers. Feathers were not clipped in this process. The adhesive set within 3–5 min. depending on ambient temperature. The transmitter was not visible on the birds and the whip antenna was very difficult to see even with binoculars at close (<20 m) distances during daylight. The bird was replaced in the roost site with the spotlight off and restrained momentarily until quiet. The investigator was able to back from the area without flushing the plover. Transmitters remained attached a minimum of two months, with some lasting up to four months.

Transmittered birds were relocated as frequently as possible using a hand-held three-element yagi antenna and TRX-1000 Wildlife Materials Inc. (Carbondale, Illinois) receiver. For the most part, however, relocations from the ground were very difficult (signal range <700m), especially in the flat terrain of the San Joaquin Valley. Most relocations were made using dual antennas from an aircraft flying transects spaced 32 km apart. We easily picked up transmitter signals from birds within this 16-km distance. One signal was detected at >60 km.

Specific locations of plovers were recorded using the Magellan NAV 5000 Global Positioning System (Magellan Systems Corporation, San Dimas, California). Position readings were only recorded if a satellite geometric quotient registered ≥7 on a scale of 1–9. Accuracy of our specific machine using this technique was calculated at 7.2 ± 1.4 (SD) m latitude and 8.4 ± 1.6 m longitude based upon locations at a known (surveyed) benchmark.

The habitat at the site of each plover relocation was recorded. All relocations of birds were plotted on standard U.S. Geological Survey maps. We calculated minimum movement distances of plovers at each study area as the straight-line distance between successive locations. For each study area we determined the availability of habitats to plovers by plotting distances from the capture site for all plover relocations (n = 168 and n = 281 at Pixley NWR and Carrizo Plain, respectively) and truncated the greatest 5% of the distances as outliers that would have strongly biased the analyses. We calculated a mean greatest distance of relocation among birds. This mean greatest distance of movement from the capture site was used to delineate a plover-defined area of use. Plover use of habitats at the Pixley NWR were compared to those available as quantified from mappings of Southern San Joaquin Valley Ecosystems (Anderson et al. 1991), which was ground-truthed at the scale of 65 ha. Generally, however, most habitat types in the Pixley NWR region occurred in regular blocks of 259 ha. A similar technique to define habitat use patterns was employed at the Carrizo Plain using aerial

photographs with ground validations to quantify available habitats.

RESULTS

Plovers began to arrive in California in October. On the Pixley NWR, birds were first reported on 20 October 1992 and 17 October 1993 (J. Engler, pers. comm.). On the Carrizo Plain plovers were first seen on 18 October 1992 (D. Germano, pers. comm.) and 7 October 1993. Generally, large numbers of plovers were not seen until after 1 November each year at either area. We began looking for plovers to capture in late October each year.

We transmittered 21 plovers on the Pixley NWR from November 1992 through January 1993. Of those, 12 were captured on an accidentally burned non-native grassland site; the other nine were captured on an adjacent agricultural field that had recently been plowed. One bird was never relocated, probably due to transmitter failure.

A total of 24 plovers were transmittered on the Carrizo Plain from November 1993 through January 1994. The U.S. Bureau of Land Management conducted 2 experimental burns to attract plovers, and 6 birds were captured on those burns. The remaining birds were captured on alkali flats ($n = 8$) and heavily grazed grasslands ($n = 10$).

SURVIVAL

We recorded no mortalities of birds at the Pixley NWR study area. One transmittered bird was preyed on at the Carrizo Plain apparently by a San Joaquin kit fox (*Vulpes macrotis mutica*) based upon presence of fox scat at the site. A second mortality of an unmarked plover was recorded at that study area, also apparently killed by a fox. Both mortalities were on alkali flat habitats. We calculated daily survival rates (Heisey and Fuller 1985) of wintering Mountain Plovers as 0.9996 based upon 2,395 days of relocations of 44 transmittered birds across the two field seasons. The calculated survival probability for the 1 November to 15 March winter period was 0.9474.

FLOCKING PATTERNS

Two plovers were observed as solitary individuals. Otherwise, plovers foraged and roosted in flocks ranging from 2 to >1,100 individuals throughout the winter. Birds roosted in closer proximity to flock members than when they foraged. We also noted that roosting birds were in tighter flocks during periods of heavy fog and rain.

Mean flock size increased through both seasons (Pixley NWR: $F = 4.3$, $P = 0.001$; Carrizo Plain: $F = 2.8$, $P = 0.025$) with the largest flocks being observed in March just prior to spring migration (Table 1). Of 170 relocations at the Pixley NWR, two birds remained together for three days. Otherwise, all birds were located in flocks with no other transmittered birds even though birds were always captured, transmittered, and released in flocks of 2–5 birds. No birds were ever relocated together ($n = 281$ relocations) on the Carrizo Plain where birds were captured in flocks of 2–6 birds. Clearly, flocks were loosely organized with individuals departing and arriving freely.

ROOSTING BEHAVIOR

At the time of detection, most roosting plovers were crouched in depressions with the entire tarsus against the surface (Fig. 1). These depressions were occasionally found in areas of fossorial mammal activity, but generally consisted of weathered hoof prints made by cattle that had been in the area when the surface was muddy. We measured 13 such depressions used for roosting as having dimensions of 22.8 ± 4.7 (SD) cm long, 15.2 ± 4.0 cm wide, and 6.8 ± 2.5 cm deep. We also noted that seven birds roosting on plowed fields roosted in furrows that were 30.5 ± 11.2 cm wide and 13.2 ± 13.0 cm deep. Birds generally roosted with the eyes just visible above the horizontal plane. The only locale where birds were not found roosting in depressions was on alkali flats on the Carrizo Plain where such depressions were not present.

MOVEMENT PATTERNS

We relocated the 20 plovers at Pixley NWR on 168 occasions for 797 plover-days of information. The average distance an individual plover moved varied from 0.2 to 1.9 km/day (Table 2). The longest, straight-line distance (i.e., the shortest possible move) between successive relocations of a bird was 28.3 km between 30 December 1992 and 8 January 1993. This move, however, may have only poorly reflected the dispersal capabilities of birds on a week-to-week basis. The aerial searches that season were limited in scope, extending only 64 km from the

TABLE 1. Mean (±SD) number of Mountain Plovers in wintering flocks located October 1992 through March 1993 at the Pixley National Wildlife Refuge and October 1993 through March 1994 on the Carrizo Plain of California.

	Pixley NWR		Carrizo Plain	
	n	$\bar{x}$ ± SD	*n*	$\bar{x}$ ± SD
October	11	56 ± 78.0	9	17 ± 16.1
November	15	49 ± 48.8	11	24 ± 19.3
December	30	89 ± 133.1	8	58 ± 63.6
January	33	42 ± 61.3	17	75 ± 97.7
February	50	90 ± 109.9	5	106 ± 83.1
March	18	178 ± 155.1	8	124 ± 98.0

initial capture site on the refuge. On four occasions plovers disappeared from the search area only to reappear the following week indicating potential movements of >90 km from the refuge (>60 km from the search pattern).

The second season, we relocated 24 plovers 281 times for 1,598 plover-days of information for the Carrizo Plain. Mean daily distance moved between relocations varied from 0.1 to 9.5 km. The expanded search pattern at Carrizo confirmed the 1993 suspicions of longer routine movements by plovers within Central California. We recorded birds moving >55 km on seven different occasions. The longest plover move between relocations was 127 km over the Temblor Mountains and into the Tulare Basin of the San Joaquin Valley between 29 December 1993 and 5 January 1994. In 1994, nine plovers moved from the Carrizo Plain to the San Joaquin Valley. Two of those plovers subsequently moved back to the Carrizo.

Despite the tendency for some birds to make long moves, the majority of wintering plovers were fairly localized in their daily activities. Of the 44 transmittered birds, 38 showed a mean move of ≤1.6 km/day; 30 birds moved ≤1.0 km/day. The mean minimum move for all relocated birds was 1.17 ± 1.42 km/day. Plovers at Pixley NWR moved 0.83 ± 0.50 km/day compared to Carrizo Plain birds moving 1.45 ± 1.84 km/day, the difference not supported statistically ($t = 1.6$; $P = 0.12$).

HABITAT PREFERENCES

Mountain Plovers at Pixley NWR immediately began using freshly tilled fields as they became available in early December. For the entire season, plovers were recorded on native habitats on

TABLE 2. Minimum mean distance moved daily by radio-telemetered Mountain Plovers at Pixley NWR, 1992–1993, and on the Carrizo Plain, 1993–1994, California. Mean distances were calculated based upon the total number of days that the bird was known to carry a transmitter in the area, not on the number of confirmed relocations.

Bird number[a]	Days	Distance $\bar{x}$ ± SD
Pixley NWR (1992–1993)		
1	33	0.6 ± 1.85
2	54	1.0 ± 2.90
3	18	0.3 ± 1.24
4	34	0.2 ± 0.67
5	38	1.1 ± 3.24
6	59	0.5 ± 1.88
7	49	0.5 ± 1.21
8	67	0.5 ± 1.92
14	11	0.9 ± 1.01
15	31	0.7 ± 1.47
16	84	1.4 ± 4.61
17	11	0.6 ± 0.88
18	15	1.0 ± 2.66
19	35	1.9 ± 4.78
20	2	0.4 ± 0.18
21	11	1.0 ± 2.75
23	13	0.3 ± 0.97
24	33	0.5 ± 1.85
25	49	1.8 ± 3.49
27	84	1.5 ± 3.92
Carrizo Plain (1993–1994)		
75	109	1.3 ± 6.98
76	116	0.6 ± 1.93
77	63	0.6 ± 1.83
78	58	0.8 ± 2.47
79	79	1.0 ± 5.24
81	15	0.5 ± 1.22
82	51	0.6 ± 2.89
83	64	0.8 ± 2.41
84	20	9.5 ± 28.5
85	25	0.7 ± 2.27
86	97	1.0 ± 3.53
87	105	2.5 ± 11.9
88	101	1.2 ± 4.05
89	93	1.7 ± 7.76
90	63	1.4 ± 5.27
91	28	0.1 ± 0.28
92	36	0.8 ± 2.30
93	70	1.0 ± 4.75
94	62	2.9 ± 9.49
95	68	0.8 ± 2.95
96	31	0.6 ± 1.42
97	59	1.3 ± 4.60
98	124	0.7 ± 4.06
99	61	2.6 ± 8.59

[a] Number corresponds to last digits of U.S. Fish and Wildlife Service band.

35.7% of relocations and on plowed ground 64.2% of relocations.

We calculated a plover-defined study area with a radius of 11.0 km as 381 km² centered on Pixley NWR. This area held 359 km² of potential habitat (flat, terrestrial landscape) comprising 331 km² (92%) of agricultural land and 28 km² (8%) of grasslands. The grasslands included 1.9 km² of grasslands that had recently burned.

Describing habitat preference based upon all relocations of birds was misleading because individual plovers were located a variable number of times. To avoid a few birds dominating the habitat-use patterns (Aebischer et al. 1993), we used only eight randomly selected relocations/individual, which gave us information from eight plovers. Plovers showed strong preferences for native grasslands over agricultural lands (χ^2 = 17.4, 1 df, $P < 0.001$) and burned areas over unburned areas (χ^2 = 208.0, 1 df, $P < 0.001$) within grasslands.

The second season, we increased the frequency of aerial reconnaissance on the Carrizo Plain and calculated a plover-defined area for the Carrizo with a radius of 26.7 km as 2,240 km². Owing to much rugged terrain within the area, however, only 201 km² was potential habitat. This potential habitat included 23 km² (11.5%) of agricultural land, 173 km² (86.5%) of grasslands, and 5 km² (2%) of alkali surfaces. The grasslands included 0.5 km² of grasslands that were experimentally burned to attract plovers.

We randomly selected eight locations from each of 13 plovers for habitat-use comparisons. Plovers again showed strong preferences for native habitats over agricultural lands (χ^2 = 7.6, 1 df, $P = 0.01$). They also showed a preference for alkali and burned areas within grasslands (χ^2 = 49.6, 1 df, $P < 0.001$), whereas there was no preference for alkali vs. burn areas (χ^2 = 0.9, 1 df, $P = 0.75$).

TIME OF DEPARTURE

The last aerial survey for plovers in the spring of 1993 was conducted on 24 February. After that date we visually monitored the numbers of birds in an alkali flat south of the town of Allensworth where birds both foraged and roosted. That flock peaked at 696 birds on 6 March and subsequently declined daily with the last bird being seen on 18 March.

In 1994, we were able to document specific departure dates for eight birds that were radio-transmittered and being relocated daily: two departed 10 March, one on 16 March, and five on 18 March. One transmittered bird was in a flock of 257 on 15 March. That bird was in the same area in a flock of 204 birds on 16 March, but presumably left that evening as it was gone on the morning of 17 March. A large flock in excess of 200 plovers was still in the vicinity on 18 March, implying that plovers migrate in relatively small flocks. Two additional birds with transmitters departed sometime between 19 and 26 March, but exact dates of departure were uncertain.

DISCUSSION

Mountain Plovers are generally considered to winter from Texas and eastern Mexico to California and Baja California Sur on the west. We are aware of recent winter sightings of plovers in Tamaulipas and Baja California. Migratory routes of the species are unknown.

At least some of the California plovers were known to breed in Colorado. We color-banded 338 birds (20 nesting adults, 318 chicks) on breeding grounds in many western states from 1990 through 1992. In 1992, two birds banded on the Pawnee National Grasslands in Weld County, Colorado, were sighted in California. An immature was seen on the Carrizo Plain on 30 October and an adult on the Pixley NWR on 7 November. None of 50 birds color-banded in California from autumn 1992 through spring 1994 has been sighted on the breeding grounds.

The habit of Mountain Plovers roosting in depressions was reported previously for fledglings in Kansas (Ptacek and Schwilling 1983). This behavior has also been reported for Piping Plovers (*C. melodius*) (Haig 1990) and Snowy Plovers (*C. alexandrinus*), the latter also roosting behind surface objects on beaches (G. Page, pers. comm.). Use of depressions by those species is believed to be a thermoregulatory behavior to avoid offshore breezes (S. Haig and G. Page, pers. comm.). The Mountain Plover winters inland, however, generally in wind-free arid landscapes. In addition, there are heavy fog inversions in the San Joaquin Valley from approximately 1 December to 1 March. Whereas the only two predations of plovers that we observed occurred on the depression-free alkali flats of the Carrizo Plain, we speculate that roosting in depressions serves (at least partially) as an adaptation by birds to avoid

detection by predators. The speculation is supported by the observation that anti-predator behavior of plovers often includes crypsis, both by chicks (Sordahl 1991) and adults. When initially disturbed, non-breeding adult birds often calmly turn their backs, slowly sit down, and remain motionless rather than taking flight.

FLOCKING AND MOVEMENTS

Mountain Plovers foraged and roosted in loose flocks. The composition of these flocks changed frequently. Birds transmittered together from a single flock were almost never found together at subsequent relocations.

The tendency towards loose flock organization reflected highly variable movement patterns of individual birds. Some plovers remained at sites for prolonged periods, with the majority of birds moving <1 km/day. Other birds were much more mobile. The variability within daily movement patterns reflected the tendency of birds to relocate to new foraging/roosting areas then usually remain in that area for a number of days.

Infrequent movements by plovers between the Carrizo Plain and Southern San Joaquin Valley likely occurred in the first year but would have gone undetected as our aerial reconnaissance did not include the Carrizo Plain. Such movements across the Temblor Mountains were, however, picked up the second year. Two birds moved from the Carrizo Plain to the Valley then returned to the Carrizo Plain at a later date. The loose flock structure coupled with these types of movements indicate that year-to-year fidelity to specific sites is poorly developed in this species during the winter months. Further, we conclude that the Carrizo Plain and San Joaquin populations are biologically sympatric, as may be the entire Central Valley population.

NATIVE HABITATS

Plovers showed very strong habitat preferences on the study areas. In order, they preferred alkaline flats, recently burned fields, and those grassland landscapes where the vegetation was heavily grazed by domestic livestock or populations of fossorial mammals as giant kangaroo rats (*Dipodomys ingens*) and California ground squirrels (*Spermophilus beecheyi*) that occur in locally high densities. Plovers preferred burns as night roosting sites (probably to avoid predators) but rarely foraged in burned fields.

Mountain Plovers seemed to prefer the Valley Sink Scrub vegetative association that is characterized by heavy, saline/alkaline clays of historic lakebeds and playas. At lowest elevations, shrub density in this association was very sparse to non-existent. The soils crack when dry and we have observed plovers probing those cracks for terrestrial invertebrates.

The other main vegetative association used by Mountain Plovers was historically the California prairie that is presently a Non-native Grassland. This association is dominated by annual grasses and forbs which also occur on fine-textured, usually clay soils. The landscape generally lacks shrubs and historically was the domain of the giant kangaroo rat (Grinnell 1932). Both the Valley Sink Scrub and Non-native grasslands are now nearly extirpated owing to flood control, agricultural development, and ground water pumping. Plovers at both the Carrizo Plain and Pixley NWR appeared to be dependent upon core areas of these native landscapes. Such areas in the Pixley NWR vicinity were especially critical early in the season before farmers began to cultivate fields.

USE OF CULTIVATED LANDS

Mountain Plovers in the San Joaquin have long been known to forage and roost on flat, recently cultivated lands (Grinnell and Miller 1944). Although telemetered plovers at the Pixley NWR were predominantly relocated on cultivated lands, we conclude that they are being forced to use tilled fields because of the loss of native habitats in the San Joaquin Valley.

A question remains as to why plovers might view cultivated landscapes as acceptable alternate habitats to open, flat, native landscapes. A possible explanation is the historic high densities of kangaroo rats in the San Joaquin Valley and on the Carrizo Plain. The denuded and disturbed surface of the rat precincts strongly resembles the micro-relief in prairie-dog (*Cynomys* spp.) towns used by breeding plovers at many locales on the Great Plains (Knowles et al. 1982, Olson-Edge and Edge 1987). In addition, the kangaroo rat precincts were highly disturbed historically by the predatory excavations of badgers (*Taxidea taxus*). Grinnell et al. (1937: see Fig. 138) described badger excavations at a local density in Kern County of 2–4/m^2, giving the appearance of a recently plowed field.

DEPARTURE AND SPRING MIGRATION

Plovers appeared to move to staging areas where flocks of 600–800 birds were not uncommon. These moves occurred primarily in late February and early March. Most birds appeared to leave California in mid-March, probably in flocks of <100 birds. Whereas plovers regularly and predictably arrive on the Pawnee National Grasslands on or shortly after 17 March, birds appear to make a nonstop flight to the breeding grounds. This speculation is corroborated by the historical absence of sightings of migrating plovers in the Great Basin in the spring (e.g., Behle and Perry 1975, Hayward et al. 1976).

WINTERING ECOLOGY RELATIVE TO POPULATION DECLINES

The decline in the continental population of Mountain Plovers since 1966 has been relatively universal across all breeding areas (Knopf 1994). Despite the extensive fragmentation of the Great Plains by agriculture, reproductive rates and success of plovers appear stable in native habitats (Miller and Knopf 1993). Those authors concluded that the declines either represent a continuation of longer term declines on breeding areas or reflect problems in migration or wintering habitats.

Overwinter survival of plovers appears to be high in California. However, native wintering habitats in the San Joaquin Valley especially appear to be limited with most sites having been converted to cropland. Virtually all alkaline flats, highly preferred habitats, have been manipulated to leach salts from the soil to facilitate conversion to cropland. Whereas plovers coevolved in breeding habitats of extensive shortgrass prairie locally disturbed by prairie dogs (*Cynomys* spp.), 30–60 million bison (*Bison bison*), and pronghorn (*Antilocapra americana*), in California they seemed to have wintered in similar landscapes dominated by kangaroo rats, 500,000 Tule elk (*Cervus elaphus nannodes*) (McCullough 1971), and pronghorn. Plovers currently wintering further south in the Imperial Valley of California appear to use cropland almost exclusively. There, they can usually be found on fields that have been recently harvested and then either burned or grazed by domestic herbivores.

Considering the high overwinter survival rate and the ability of plovers to use non-native habitats we conclude that loss of a major proportion of native habitats has not limited plover populations. Thus, continental declines appear attributable to longer-term processes on the breeding grounds. Nonetheless, the preservation of core areas of native habitats as at Pixley NWR during the early winter appears critical to support wintering plovers, especially in the San Joaquin Valley where freshly cultivated fields are not available early in the season. The potential role of pesticide contaminants in California needs to be addressed.

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LITERATURE CITED

AEBISCHER, N. J., P. A. ROBERTSON, AND R. E. KENWARD. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

ANDERSON, R. L., L. K. SPIEGEL, AND K. M. KAKIBA-RUSSELL. 1991. Southern San Joaquin Valley ecosystems. California Energy Comm. P70091-004. Sacramento, CA.

BEHLE, W. H., AND M. L. PERRY. 1975. Utah birds. Utah Museum of Natural History, Univ. of Utah. Salt Lake City, UT.

GRAUL, W. D. 1975. Breeding biology of the Mountain Plover. Wilson Bull. 87:6–31.

GRAUL, W. D., AND L. E. WEBSTER. 1976. Breeding status of the Mountain Plover. Condor 78:265–267.

GRINNELL, J. 1932. Habitat relations of the giant kangaroo rat. J. Mammal. 13:305–320.

GRINNELL, J., J. S. DIXON, AND J. M. LINSDALE. 1937. Fur-bearing mammals of California, their natural history, systematic status, and relations to man. Univ. of Calif. Press. Berkeley, CA.

GRINNELL, J., AND A. H. MILLER. 1944. The distribution of the birds of California. Pacific Coast Avifauna 27.

HAIG, S. M. 1990. Piping Plover, *Charadrius melodus*, p. 1–16. *In* A. Poole and F. Gill, [eds.], The birds of North America, No. 2. The Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, DC.

HAYWARD, C. L., C. COTTAM, A. M. WOODBURY, AND

H. H. FROST. 1976. Birds of Utah. Great Basin Nat. Memoirs 1:1–229.

HEISEY, D. M., AND T. K. FULLER. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. J. Wildl. Manage. 49:668–674.

KNOPF, F. L. 1994. Avian assemblages on altered grasslands. Stud. Avian Biol. 15:247–257.

KNOPF, F. L., AND B. J. MILLER. 1994. *Charadrius montanus*—montane, grassland, or bare-ground plover? Auk 111:504–506.

KNOWLES, C. J., C. J. STONER, AND S. P. GIEB. 1982. Selective use of black-tailed prairie dog towns by Mountain Plovers. Condor 84:71–74.

MCCULLOUGH, D. R. 1971. The Tule elk: its history, behaviour and ecology. Univ. Calif. Publ. Zool. 88:1–191.

MENGEL, R. M. 1970. The North American Central Plains as an isolating agent in bird speciation, p. 280–340. *In* W. Dort and J. K. Jones, [eds.], Pleistocene and recent environments of the central Great Plains. Univ. of Kansas Press, Lawrence, KS.

MILLER, B. J., AND F. L. KNOPF. 1993. Growth and survival of Mountain Plovers. J. Field Ornithol. 64:500–506; 65:193.

OBERHOLSER, H. C. 1974. The bird life of Texas. Univ. of Texas Press. Austin, TX.

OLSON-EDGE, S. L., AND W. D. EDGE. 1987. Density and distribution of the Mountain Plover on the Charles M. Russell National Wildlife Refuge. Prairie Nat. 19:233–238.

PTACEK, J., AND M. SCHWILLING. 1983. Mountain Plover reintroduction in Kansas. Kansas Ornithol. Soc. Bull. 34:21–22.

SHACKFORD, J. S. 1991. Breeding ecology of the Mountain Plover in Oklahoma. Bull. Okla. Ornithol. Soc. 24:9–13.

SORDAHL, T. A. 1991. Antipredator behavior of Mountain Plover chicks. Prairie Nat. 23:109–115.