

NEW WORLD SECTION



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BEHAVIORAL ECOLOGY OF THE MOUNTAIN PLOVER IN NORTHEASTERN COLORADO

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INTRODUCTION

Breeding behavior among shorebirds runs the gamut from lek polygyny to monogamy to resource defense polyandry (Pitelka et al. 1974, Jenni 1974, Oring 1982). The relative prevalence of polygamous mating patterns in this group apparently stems from two aspects of its natural history: 1) young are precocial and able to feed themselves, and 2) clutch sizes are small and determinate. These factors, at least in some instances, allow a single parent to raise the brood alone. The emancipated parent may then be able to attempt subsequent reproductive efforts. This note reports on the initial stages of a study of the rapid multi-clutch breeding system of the Mountain Plover *Charadrius montanus*. This mating system, in which both sexes mate more than once, has been reported in the Mountain Plover (Graul 1973), the Temminck's Stint *Calidris temminckii* (Hilden 1975), and the Sanderling *C. alba* (Parmelee and Payne 1973). It is suspected to occur also in the Little Stint *C. minuta* (Pitelka et al. 1974). In its simplest form, a female produces a clutch of eggs which is incubated by the male alone. She then produces a clutch of eggs which she incubates alone. The second clutch may or may not be sired by her initial mate. In all three species in which this system has been documented clearly, males may delay incubation of their first clutch while courting and mating with females other than their first mate. Thus mating patterns in the rapid multi-clutch system incorporate elements of both polyandry and polygyny.

This mixing of mating patterns within a single species suggests that the rapid multi-clutch system may represent an evolutionary cross-road between monogamy and some form of polygamy. Depending upon a number of social and ecological factors, such a system could evolve into either polyandry or polygyny. These divergent evolutionary outcomes reflect the marked differences between the fitness-maximizing strategies of males and females in rapid multi-clutch species. By monitoring mating patterns in a population of Mountain Plovers on the short-grass prairie of north-eastern Colorado, we hope to shed light on the dynamics of these intersexual conflicts.

STUDY SITE

Our research in 1983 was conducted on the Pawnee National Grassland in Weld County, Colorado. A brief summary of the topography, vegetation, and climate of this region was provided by Graul (1973). Precipitation patterns on this short-grass prairie are

notoriously variable (Graul 1973), and 1983 was no exception. Precipitation data recorded by the Central Plains Experimental Range (CPER) since 1970 indicate that the first half of 1983 (1 January - 30 June) was the wettest such period on record, with precipitation 159% of the 14-year mean. In addition, severe late spring storms persisted into May, with up to 0.3 m of snow falling on the Pawnee as late as 17 May.

Field work on Mountain Plovers occurred from 2 March to 2 April and from 16 May to 13 July. In March and April field work was conducted throughout the Pawnee to locate plovers and identify potential study sites. From May to July field work was concentrated at 2 sites, Wildhorse Valley and Bull Valley. A third site at Lynn Lake was visited occasionally. The sites are described below.

Wildhorse is located along Weld County Rd. 96 just west of Rd. 61. The Wildhorse site comprised approximately 190 ha between 1535 m and 1575 m in elevation. In addition to the dominant association of blue gramma *Bouteloua gracilis* and buffalo grass *Buchloe dactyloides*, the prairie prickly-pear *Opuntia polyacantha* was especially common. Less abundant was four-winged saltbush *Atriplex canescens*, and rarer still was prairie yucca *Yucca glauca*. There was no permanent water at this site, although the abnormally wet spring resulted in a few swales that remained marshy into early June. Cattle grazed occasionally on the study site; their activity was concentrated near a watering tank north of Rd. 96.

Bull Valley. This 360 ha study site also straddled Rd. 96, and was centered 4 km east of Wildhorse. Three intermittent streams drained the site in early summer, but were dry by July. The entire area was used regularly by cattle, with especially heavy grazing activity occurring on flats bordering the streams. The upper portion of the eastern stream was also heavily grazed by a small resident prairie dog population. Except for a higher abundance of *Atriplex*, the vegetation was very similar to that at Wildhorse. There was a similar range in elevation at Bull Valley (1520 - 1560 m), and there were 2 cattle watering tanks.

Lynn Lake. Located on the CPER 4 km east of U.S. Hwy 85, and just north of County Rd. 114, the Lynn Lake basin was the site of intensive ecological investigation from 1969 - 1974 as part of the US/IBP Grassland Biome Programme. A description of the area is provided in several of the IBP Programme's Technical Reports (e.g. Mitchell 1971).

BANDING

Between 3 June and 7 July, we captured and banded 124 Mountain Plovers (48 adults and 76 chicks). Only adults attending clutches or broods were captured, using a modification of the tent-shaped mist-net trap described by Graul (1979). Each plover was given a U.S. Fish & Wildlife Service metal band below the tarsometatarsal joint of its left leg. In addition, 4 color bands were affixed below the joint, 2 on each leg, to provide a unique color combination for each individual. The 6 colors used were red, blue, orange, yellow, mauve and light green. The 2 color bands on the right leg designate the year code. All adults banded in 1983 had either yellow over red, or blue over orange on their right leg; all chicks had red over red, green over green, or mauve over mauve on their right leg. Any reports of color-banded Mountain Plovers either on or away from their breeding grounds would be extremely valuable and greatly appreciated. Please send information concerning such sightings to B.J. McCaffery.

Weight, culmen length, and tarsal length were recorded for approximately half of the adults captured (Table 1). The mean body weight of 24 adults in our population was significantly lower than that of 15 adults recorded by Graul (pers. comm.) in his study population located 32 km southeast of our study site (means of 94.1 g vs. 106.8 g, $t = 4.65$, $P < .001$). Several factors may account for this. Although unlikely over such a short distance, it is possible that there is geographic variation in body weight between local populations. More plausible is the possibility that the unusually inclement spring weather reduced prey abundance, leading to a decrease in foraging efficiency, and subsequently reducing body weight at our site. Another possibility is that female Mountain Plovers may be heavier than males (Graul pers. comm.); perhaps our sample was biased toward males if few females tended clutches of their own in 1983. A final hypothesis to explain the discrepancy between our data and that of Graul is that breeding plovers may lose weight during the breeding season, as has been reported in other shorebirds (Pitelka 1959, Ashkenazie and Safriel 1979). Graul collected weight data throughout the breeding season, whereas our measurements were taken only during the latter half, when most birds may be lighter. The steady decline during the season in the body weights we recorded (Table 2) lends support to this hypothesis.

Table 1. Biometrics of adult Mountain Plovers captured on the Pawnee National Grassland, Colorado, in 1983.

	N	Mean	SD
Weight	24	94.1 g	6.61
Culmen	24	21.8 mm	1.08
Tarsus	24	40.7 mm	1.94

Table 2. Mean weights by week of adult Mountain Plovers captured on the Pawnee National Grassland, Colorado, in 1983. All data points represent different individual birds (i.e. no adults were weighed more than once).

Week	N	Mean Wt. (g)	S.D.
12 June - 18 June	10	98.6	6.36
19 June - 25 June	6	91.3	6.86
26 June - 2 July	4	90.8	2.99
3 July - 9 July	4	90.3	2.99

BREEDING BIOLOGY

A few Mountain Plovers had already appeared on the Pawnee by our arrival on 24 March. At first, only twosomes and trios were observed, but by 30 March loose flocks of up to 10 plovers were noted. These early arrivals were seen almost exclusively on fairly level heavily grazed areas, as reported by Graul (1973). The first aerial breeding displays were observed on 27 March and ground courtship displays culminating in copulation were first observed on 1 April. During the last week of March, foraging plovers were repeatedly seen capturing the late instars of the band-winged grasshoppers *Xanthippus corallipes* and *Arphia conspersa*. Foraging seemed to occupy a small portion of the plover's time, suggesting that they are not energetically stressed when they arrive on the breeding grounds.

On 3 consecutive evenings (29-31 March), BJM observed different flocks of foraging plovers at different locations, to determine whether they gather into nocturnal roosts. Each evening, foraging plovers stopped feeding as much as 90 min before darkness, and coalesced into loose roosting flocks of up to 10 individuals. At 1835 (+ 2 min) the flock members stood up, foraged briefly, and then flew off. Whether this behavior was an antipredator strategy, a prelude to nocturnal migration by transient birds, or a movement of local birds to larger roosts, could not be determined because sufficient light for observations disappeared at precisely the same time as the birds.

When we returned to the study area in mid-May, plovers were markedly less conspicuous than on our previous trip. Plovers were absent from several localities where courtship and territorial behavior had been observed regularly in late March and early April. Perhaps the early observations were of migrating transients, or perhaps breeding efforts in these areas were abandoned. In either case, densities were extremely low. Wide-ranging censuses throughout the western Pawnee on 25-26 May, covering 372 ha of suitable habitat, yielded only 4 plovers (1/km²). Graul and Webster (1976) provided rough estimates of breeding density on the Pawnee in areas of varying habitat quality. Even using the lowest density figures and most conservative assessment of habitat quality, their estimates indicate minimum densities twice as high as our census results. However, the densities recorded on our large-scale censuses contrasted sharply with the locally high densities observed in our 2 main study areas. Although no formal censuses were conducted there, our field work indicated densities of 15-20 plovers/km².

The plovers observed in May were also found in a wider variety of habitats than those noted in March. Plovers foraged and displayed on slopes and ridges as well as flats, and they were not restricted to heavily grazed areas. Plovers were found regularly in areas currently subject to only moderate grazing pressure and having extensive stands of *Opuntia*, *Atriplex*, and various species of wildflowers. In addition, both adults and chicks were found sometimes in plowed fields.

To determine the phenology of clutch initiation, laying dates were calculated by back-dating from hatching dates at nests, and a similar method was used for broods by estimating the age of the chicks (see Graul 1975, p.10). Estimated clutch initiation dates ranged from 1 May to 30 May. The earliest known hatching date was 6 June, with the last active nest hatched on 26 June. Our clutch initiation data are plotted along with Graul's (1975) in

Table 3. Nest fates in 1983 (present study), compared with 1969 and 1971 (Graul 1975).
The fates of 2 nests in 1983 were unknown.

Year	Fate of Nests									
	No.	No.	Eggs				Crushed	Human	Weather	
	Nests	Eggs	Hatched	Hatched	Depredated	by Cow	Disturbance	Losses	Abandoned	
1983 (present study)	26	76	19	9	9	1	4	0	1	
1971 (Graul 1975)	21	-	-	10	3	0	2	0	6	
1969 (Graul 1975)	80	-	-	52	11	0	7	10	0	

Table 4. Mean number of Mountain Plover chicks per brood observed in 1983.
Fledging occurs at about 33-34 days of age (Graul 1975).

Estimated age (in days)	1-5	6-10	11-15	16-20	21-25	26-30
Number of broods	25	8	4	1	3	3
Mean brood size	2.16	1.75	1.5	1	1.67	1.33

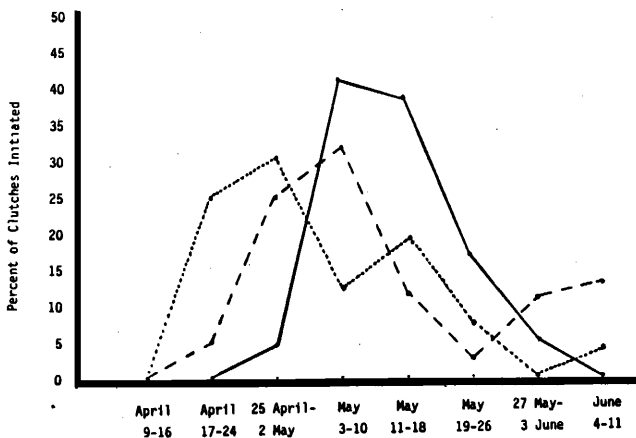


Figure 1. Phenology of nest initiations in 1969, 1971 and 1983. Dotted line = 1969 (Graul 1975, n=55), dashed line = 1971 (Graul 1975, n=45), solid line = 1983 (this study, n=48).

Figure 1. Our earliest laying date is nearly 2 weeks later than Graul's (1 May vs. 21 April), and our last known laying date is nearly 2 weeks earlier (30 May vs. 12-15 June). The peak of laying in 1983 was also later than in either 1969 or 1971. The late initiation of nesting may have been caused by the abnormally late spring. On the other hand, the apparent delay may have been an artifact caused by the destruction or abandonment of early nests due to severe weather. The early cessation of laying is more difficult to understand since June was fairly mild and invertebrate censuses indicated that plover prey density remained stable through the middle of that month.

Twenty-six nests were discovered, and the fates of these nests are compared with Graul's data (1975) in Table 3. Since the fates of 2 nests are unknown and 4 nests were abandoned due to our disturbance, we have excluded these nests from our calculations of nesting success. Nine of the remaining 20 nests hatched at least one young (45%). At these successful nests, only 19 of 27 eggs hatched (70.1%), or 2.11 eggs per nest. In Graul's study (1975), 88.7% of the eggs at successful nests hatched, or 2.66 eggs per nest. Nine of 20 nests were depredated (45%), which is a predation rate 3 times that recorded by Graul (1975) at his Keota field site.

Chick survival was poor as well. However, chick mortality did not seem to be concentrated in

the first few days after hatching, as reported by Graul (1975). Both the average number of chicks hatched per successful nest, and average brood size in chicks 1-5 days old, was 2.1. Nonetheless, average brood size decreased steadily as chick age increased (Table 4). More dramatic was the decrease in the number of broods recorded with chicks older than 5 days, which indicates a high frequency of total brood loss. By our departure on 13 July, we had observed no fledged juveniles. On the basis of our laying phenology data, approximately one-third of the season's nests could have produced fledged young by that date.

In summary, Mountain Plover breeding success in our study area was poor due to 3 factors: 1) a restricted laying season, 2) a high rate of egg loss due to predation and low viability, and 3) high chick mortality.

ANTIPREDATOR BEHAVIOR

Potential predators of adult Mountain Plovers, chicks, and/or eggs, that have been observed on our study sites include Swainson's Hawk *Buteo swainsoni*, Rough-legged Hawk *B. lagopus*, Ferruginous Hawk *B. regalis*, Golden Eagle *Aquila chrysaetos*, Northern Harrier *Circus cyaneus*, Prairie Falcon *Falco mexicanus*, Great Horned Owl *Bubo virginianus*, Burrowing Owl *Athene cunicularia*, coyote *Canis latrans*, black-tailed prairie dog *Cynomys ludovicianus*, thirteen-lined ground squirrel *Spermophilus tridecemlineatus*, gopher snake *Pituophis melanoleucus*, and western rattlesnake *Crotalus viridis*.

Aerial predators are the most likely predators of adult plovers. Adult Mountain Plovers frequently cock their heads and look upward. When a raptor is overhead they often crouch slowly and then remain motionless. We have seen no other responses to birds of prey by plovers at any stage of the breeding cycle.

Mountain Plovers do not engage in aggressive mobbing of predators, either before or after their eggs hatch (Sordahl 1981). Plovers showed no noticeable response to decoys of a Great Horned Owl, American Crow *Corvus brachyrhynchos*, or California Gull *Larus californicus*. Although none of these potential predators of Mountain Plover adults, eggs, or chicks are common on the study area, American Avocets *Recurvirostra americana* nesting nearby mobbed the owl and crow decoys vigorously.

During the period 12 June - 12 July we sighted an average of 3.1 hawks per 10 hours. The most common species were Swainson's Hawk, Ferruginous Hawk, Golden Eagle and Prairie Falcon. Relatively few hawks were seen during the last 3 weeks of June. This was also the period during which most Mountain Plover chicks hatched. The Burrowing Owl is a common nesting species on our study area, but although it is a potential predator of plover chicks, we did not observe any responses to them by adult plovers, even when the owls hovered directly over a brood of chicks.

We observed more vigorous reactions by adult plovers to terrestrial predators. Birds with eggs usually left the nest when approached by a human and gave alarm calls from 50 m or more away. They very rarely performed distraction displays. During and after hatching, however, most birds performed vigorous distraction displays at distances of about 10-50 m. Plovers usually ignored cattle, which may occasionally step on nests (see Table 3). On one occasion, when a cow approached to within 5 m of an incubating plover, the bird performed a distraction display in which it flutter-jumped away from the cow with its wings held out much like in the Aggressive Rush posture (see Graul 1973). Mountain Plovers with eggs chased thirteen-lined ground squirrels away from nests with the Aggressive Rush posture. However, we were unable to evoke a similar response by placing a thirteen-lined ground squirrel study skin near nests or broods. One bird with chicks was seen performing a distraction display toward a coyote, flying repeatedly just ahead of it and maintaining a distance of about 15 m. The coyote did not alter its course or show any interest in the bird.

Mountain Plover chicks seem potentially vulnerable to predators, although we did not observe any predation. Both the downy and juvenal plumages are cryptic. Many chicks in both plumage classes hide when approached by humans. As with chicks of many shorebird species, there seems to be a greater likelihood that they will run as they grow older (pers. obs., Sordahl 1982). Other factors that may influence the tendency of a chick to run rather than hide are being investigated.

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REFERENCES

- Ashkenazie, S. and Safriel, U.N. 1979. Time-energy budget of Semipalmated Sandpiper *Calidris pusilla* at Barrow, Alaska. *Ecology*. 60: 783-799.
- Graul, W.D. 1973. Adaptive aspects of the Mountain Plover social system. *Living Bird* 12: 69-94.
- Graul, W.D. 1975. Breeding biology of the Mountain Plover. *Wilson Bull.* 87: 6-31.
- Graul, W.D. 1979. An evaluation of selected capture techniques for nesting shorebirds. *N. Am. Bird Bander* 4: 19-21.
- Graul, W.D. and Webster, L.E. 1976. Breeding status of the Mountain Plover. *Condor* 78: 265-267.
- Hilden, O. 1975. Breeding system of Temminck's Stint *Calidris temminckii*. *Ornis Fenn.* 52: 117-146.
- Jenni, D.A. 1974. Evolution of polyandry in birds. *Am. Zool.* 14: 129-144.
- Mitchell, G.C. 1971. *Spatial distribution and successional state of grassland vegetation related to grazing intensity treatments*. U.S. IBP Grassland Biome Programme Tech. Report 101. Colorado State University, Fort Collins.
- Oring, L.W. 1982. Avian mating systems. Pp. 1-92 in D.S. Farner, J.R. King, and K.C. Parkes, (eds.), *Avian Biology*, Vol. 6. Academic Press, New York.
- Parmlee, D.F. and Payne, R.B. 1973. On multiple broods and the breeding strategy of arctic Sanderlings. *Ibis* 115: 218-226.
- Pitelka, F.A. 1959. Numbers, breeding schedule, and territoriality in Pectoral Sandpipers of northern Alaska. *Condor* 61: 233-264.
- Pitelka, F.A., Holmes, R.T. and MacLean, S.F. Jr. 1974. Ecology and evolution of social organization in arctic sandpipers. *Am. Zool.* 14: 185-204.
- Sordahl, T.A. 1981. Predator-mobbing behaviour in the shorebirds of North America. *Water Study Group Bull.* 31: 41-44.
- Sordahl, T.A. 1982. Antipredator behavior of American Avocet and Black-necked Stilt chicks. *J. Field Ornithol.* 53: 315-325.
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