BREEDING BIOLOGY OF THE MOUNTAIN PLOVER

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The Mountain Plover (*Charadrius montanus*) is an endemic species of western North America, breeding on the shortgrass prairie mainly east of the Rocky Mountains and wintering in similar habitat from California and Texas to northern Mexico. Apart from a few anecdotal reports, detailed information on the breeding biology of the species comes from a single study (Laun 1957). In 1969, I began a study of the Mountain Plover on its Colorado breeding grounds. This paper describes various aspects of the breeding biology of the species and discusses their adaptive significance. Other aspects of the behavior of the Mountain Plover have been published elsewhere (Graul 1973a, 1973b, 1974).

STUDY AREA AND METHODS

I studied these plovers on two areas in northern Weld Co., northeastern Colorado. The major area consisted of 16 km^2 just southwest of Keota. The second area was on the International Biological Program's Pawnee Site, approximately 64 km northwest of Keota. This general area is part of the high shortgrass prairie (elevation about 1470 m) and consists of gently rolling hills with extensive flats and intermittent streams. Most observations were confined to areas covered predominantly by blue grama grass (*Bouteloua gracilis*) and/or buffalo grass (*Buchloe dactyloides*), since I observed that Mountain Plovers prefer such areas. In these areas other common plants include western wheat grass (*Agropyron smithii*), fourwing saltbush (*Atriplex canescens*), and prickly pear cactus (*Opuntia polycantha*).

The climate of the area during the breeding season is hot and dry. Average yearly precipitation ranges from 30 to 38 cm, although precipitation is unevenly distributed on a yearly, seasonal, and area-to-area basis (Badaracco 1971). The mean maximum temperatures for Grover (24 km north of Keota) are: April, 16°C; May, 21°C; June, 27.2°C; July, 30°C; August, 32.2°C. The means, however, obscure the fact that the temperature commonly reaches 37.7°C in June, July and August.

I spent the following periods on the areas: 18 March–15 August 1969; 25 May–29 May 1970; 1 June–31 July 1971; 31 March–19 May 1972; 9 May–17 May 1974. Dawn to dusk observations were made throughout most of the study and were supplemented with night observations. Most observations were made from a car using a 15 to 60× spotting scope.

I captured 43 adults at the nest or with broods and marked them with combinations of colored leg bands, numbered aluminum bands, and dye. Prior to 1974 the adults were captured with either a bow trap or a drop trap. In 1974, I supplemented these trapping techniques with a mist net funnel trap and by night lighting. To avoid nest abandonment, most trapping efforts were restricted to the hatching and chick phases. Additionally, 7 adults were marked by placing "Thief Detection Powder" (Faurot, Inc., 299 Broadway, N.Y., N.Y.) in the nest cup. These birds had to be re-marked about every three days, since the dye faded rapidly.

I found 154 nests and an additional 60 broods during the study and placed colored and aluminum leg bands on 229 chicks. In 1969 the egg position in most nests was recorded using the methods described by Lind (1961) and Drent (1967).

All positive identifications of sex were obtained through collection, laparotomy, or by observing copulatory position.

ARRIVAL, EARLY SOCIAL BEHAVIOR

The birds arrive in late March and disperse onto territories. At least some adults of both sexes occupy the same territories each year. Initial pair bonds are formed and egg-laying begins in late April. In some cases, after a female completes her clutch the male assumes all parental duties and the female produces another clutch which she attends herself. Further details concerning the events leading up to the establishment of nests are presented by Graul (1973b).

NEST SITE SELECTION

Prior to nesting several potential nest scrapes are constructed on a territory as the result of courtship (Graul 1973b). Although I do not know why one scrape is chosen over others as the nest site, it is possible to examine the features at the nests. The following is an analysis of 133 nest sites observed during 1969–72.

Vegetation type.—All nests were within the general blue grama-buffalo grass community (these two species are hard to separate except when in flower), but within this community sub-communities can be defined. Seventy percent of the nests were in areas of predominantly blue grama-buffalo grass with scattered clumps of cacti and western wheat grass, and 20% were in areas of blue grama-buffalo grass and western wheat grass patches in about equal proportions. The final 10% were located in various habitat types, mostly characterized by the presence of mixed blue grama-buffalo grass and taller vegetation such as shrubs.

Since the above analysis refers to general nesting habitat, I analyzed the vegetation within 3 m of each nest to see if birds were selecting certain features within a general habitat type. Ninety-two percent of the nests were in blue grama-buffalo grass patches.

Bradbury (1918) noted that the Mountain Plover avoids tall vegetation; my observations support this contention. The mean height of the blue grama-buffalo grass is less than 8 cm in April while the other major plant species in the habitat descriptions are over 10 cm in April.

Slope of the ground.—Sixty-five percent of the nests were on ground with less than a 1° slope and another 25% were on ground with a slope of less than 2°. Only one nest was located on ground with a 5° slope, although many of the gently rolling hills have a slope of 5° or greater. Thus, although

TABLE 1

A COMPARISON OF THE DISTANCE (CM) TO THE NEAREST COW MANURE PILE BETWEEN DIFFERENT NESTS OF THE SAME BIRD

Sex	Nest 1 (1971)	Nest 2 (1972)	Nest 3 (1972)
M	over 91	against	–
M	33	30	–
F	61	8	–
F	over 91	against	–
F	30	over 91	10

the blue grama-buffalo grass covers many of the hills in the area, Mountain Plovers nest almost entirely on flat areas, either on top of the hills or in the valleys. The same tendency has been noted in the Three-banded Plover (*Charadrius tricollaris*) (Brown 1948) and the Double-banded Courser (*Rhinoptilus africanus*) (Maclean 1967).

Proximity to manure piles.—Fifty-five percent of the nests were within 30 cm of an old cow manure pile of at least 5 cm in diameter: 19.5% were placed against a pile; 17.5% were within 7 cm of a pile; 8% were within 15 cm; 10% were within 30 cm. To determine whether the above frequency represented actual selection I sampled the distribution of cow manure piles on my study area as follows: 120 sample points were established on a transect across the overall study area and 20 of these points were randomly selected and treated as nests. None of the sample points were within 15 cm of a 5 cm diameter manure pile and only one was within 30 cm. Thus, it appears that the birds are actually selecting nest sites near old, gray cow manure piles. Individual birds, however, are not necessarily consistent in selecting nest sites in relation to cow manure piles (Table 1), so the process of such selection is puzzling.

The tendency to nest near manure has been reported for other plovers: St. Helena Sandplover (*Charadrius sanctaehelenae*) (Pitman 1965), Black-breasted Plover (*Vanellus tricolor*) (Favaloro 1944), Kittlitz's Sandplover (*Charadrius pecuarius*) (Hall 1958), Spur-winged Plover (*Vanellus miles*) (Hall 1965), and the Lapwing (*Vanellus vanellus*) (Cott 1966). In fact, nesting near manure may be an expression of a widespread tendency among Charadriidae species to nest near conspicuous objects in general. In support of the latter statement, Bunni (1959) noted that the Killdeer nested near a variety of conspicuous objects on his Michigan study area and I have noted that they frequently nest against cow manure piles on my Colorado study area.

Presence of other birds.—Another factor probably affecting the location of nests is the presence of other birds. Interspecific aggression between

McCown's Longspurs (*Rhynchophanes mccownii*), Horned Larks (*Eremophila alpestris*) and Mountain Plovers may have some spacing effects, since these species all try to drive each other away from their respective nests.

The spatial relationship of Mountain Plover nests, at least, suggests that these nests are not placed randomly with regard to each other. Even when breeding populations were high, some areas had many nests while similar areas had few suggesting a loose colonial tendency. Within a population, however, nests were widely spaced. For instance, in 1969 I attempted to find all nests on a 64.77 ha area. At one point there were 21 nests active simultaneously on this area with the average distance between Mountain Plover nests being 140 m.

EGG-LAYING PHASE

Clutch-size and egg description.—Coues (1874) noted that sometimes a Mountain Plover nest contains four eggs, but that three normally constitute the full clutch. Completed clutches I observed included one of four eggs, 134 of three eggs, 17 of two eggs, and two of one egg.

Most eggs in my study had a dark olive ground color with many black markings, similar to the description by Bent (1929). One set of eggs was distinctive in that the ground color was reddish-brown. The black marking can be: (1) bold, large blotches; (2) fine, small specks; or (3) mixtures of the two. I have no evidence that individual females tend to lay eggs with a distinctive pattern as reported for the Dotterel (*Eudromias morinellus*) (Nethersole-Thompson 1973).

Based on 58 eggs Bent (1929) listed the average measurement as 37.7 mm × 28.3 mm. I measured 114 eggs which averaged 38.1 mm × 28.6 mm. The eggs showing the four extremes in my sample measured **42.2 mm** × 28.8 mm, **34.3 mm** × 28.0 mm, 39.6 mm × **30.2 mm**, and 39.7 mm × **27.0 mm.**

Schönwetter (1967) listed the average weight of a fresh egg as 16.5 g. I found the average weight of 25 eggs during the first week of incubation was 15.6 g with a range of 13–19 g and I found no tendency for individual females to lay eggs of similar weight.

Schönwetter (1967) tabulated several egg measurements for 34 of the 37 species of Charadriinae—the relative shape of the eggs and shell thickness are especially interesting. Schönwetter expresses the roundness of an egg (K) as length divided by width. The Mountain Plover lays a more rounded, blunt egg ($K = 1.32$) than most species of Charadriinae—only three species having a lower K value. Furthermore, there is no correlation between egg shape and clutch-size, since the mean K values for the clutch-size classes are as follows: four—1.39; three—1.36; two—1.38.

Shell thickness in Charadriinae ranges from 0.12 mm–0.22 mm with only two species having shells as thick as 0.22 mm—the Mountain Plover and the New Zealand Dotterel (*Pluvialis obscura*). The thick shell in the Mountain Plover, at least, does not appear to be a direct function of egg size, since six species have a larger egg, but a thinner shell.

Laying behavior.—I observed four females laying eggs and the behavior was similar in each case. The female quickly approaches the nest, sits on it briefly, rises and moves off a few cm, then returns to settle in the scrape. One female repeated this sequence three times before settling on the nest. She then pumps her tail up and down several times, and may change position on the nest. Eventually, she rises 2 cm or so off the nest and slowly pumps her tail as the egg slowly appears. As the egg drops, her body rocks sideways noticeably. She then settles back on the nest and manipulates nest material with her beak briefly, and then leaves the nest quickly. Time spent on the nest in these four cases was 17, 21, 26, and 28 min. The time of laying in these cases was 06:30, 16:20, 18:30, and 19:14.

Laying intervals.—Data on the time intervals between successive eggs are scarce for the Mountain Plover. Laun (1957) reported a case of two eggs being laid in two days. I have recorded the following intervals between the laying of the second and third eggs: at least 28 hours (one record); 34–48 hours (eight records); 56–100 hours (one record); 96–108 hours (two records).

Laying periods and their relationship to weather.—Dates for the laying of first eggs in 1969 and 1971 were calculated by back-dating. With nests, the first egg date was determined at hatching time by allowing 29 days for incubation and three days for laying. With broods, the first egg date was determined by adding 32 days to the estimated age of the chicks where chick age was determined by comparing growth measurements with those of known-age chicks.

In 1969 and 1972 egg-laying began on 17 April, in 1971 on 21 April. In 1969 and 1971 the last clutch was started between 12 June and 15 June. As reported for many avian species (Immelmann 1971) rainy periods tended to inhibit laying, but laying frequently increased following such rainy periods (Fig. 1 and 2).

Inclement weather is likely during the first three weeks of April and this may be a factor influencing delay or start of laying until late April on average. A storm on 26 April 1972 produced 2.5 cm of snow which was then covered by sleet; the snow covered the ground for one day. Four clutches were initiated prior to this storm. One was abandoned; the others were unattended while covered by snow and incubation was resumed when the snow melted. I checked one egg in one of these nests two weeks later and it was fertile.

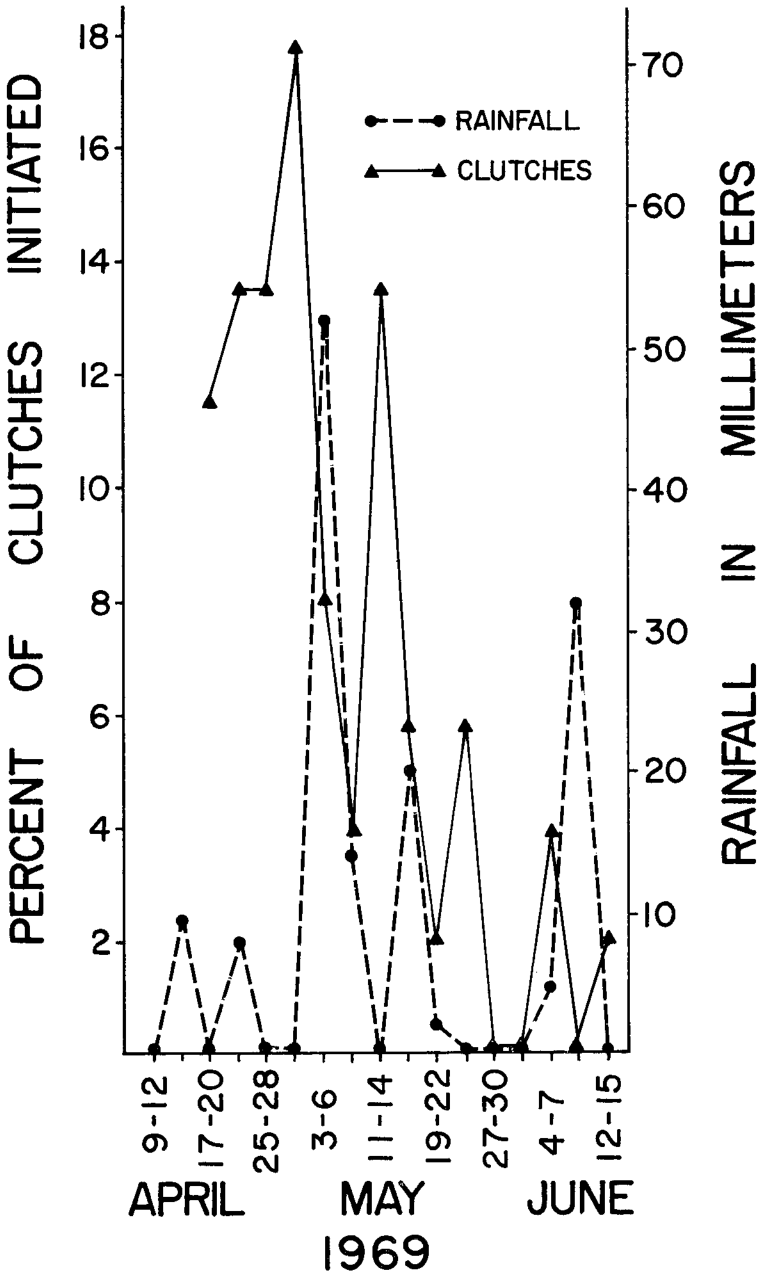

FIG. 1. Initiation of egg-laying in 55 nests in relation to rainfall in 1969.

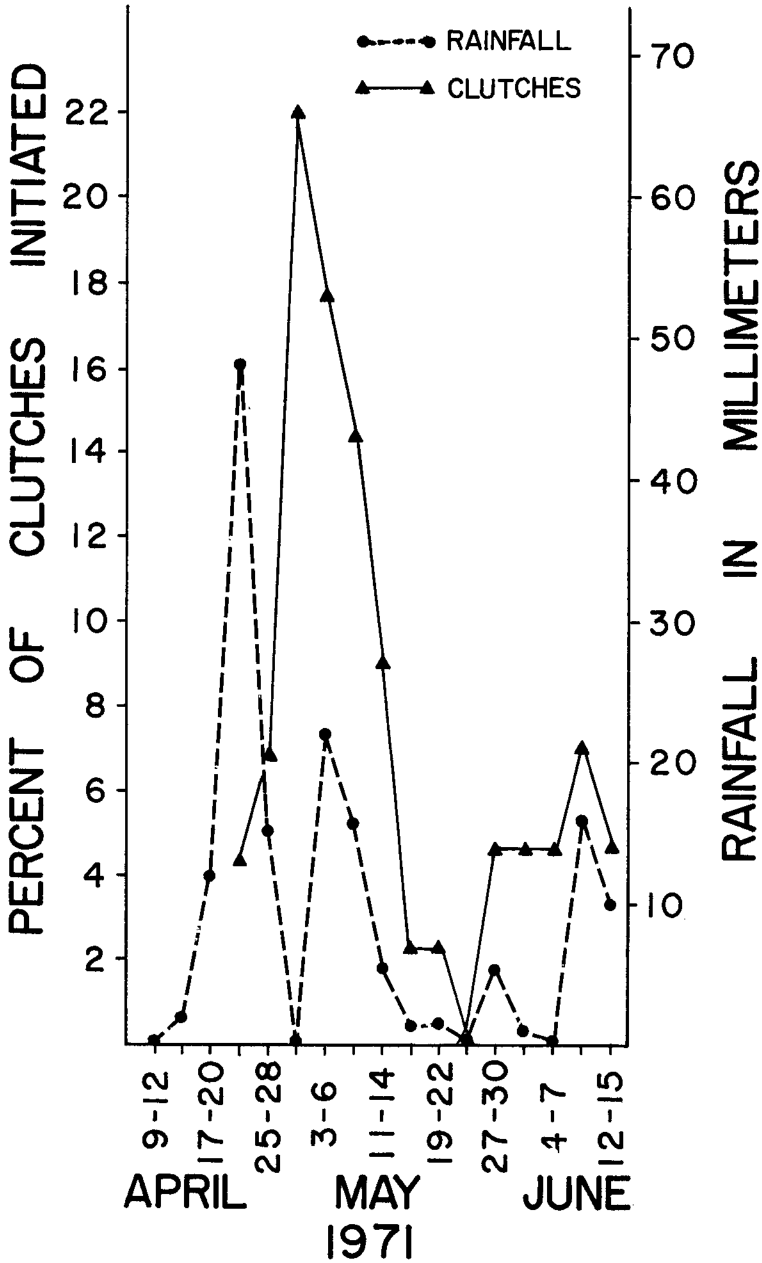

FIG. 2. Initiation of egg-laying in 45 nests in relation to rainfall in 1971.

Norton (1972) reported a set of Dunlin (*Calidris alpina*) eggs that was covered by snow for 16 hours, but hatched normally.

Weather may also be an important factor governing the end of the laying period. Most nests are initiated before mid-June, after which it commonly gets hot and dry. In 1971 June was considerably hotter and drier than in 1969 and several birds on late nests in 1971 abandoned the nests (Graul 1973b).

INCUBATION PHASE

Attentiveness.—During egg-laying the nest is attended only occasionally and attendance appears to be related to weather conditions. As in the Kentish Plover (*Charadrius alexandrinus*) (Rittinghaus 1961) and the Lapwing (Bannerman 1961), an adult will immediately come to the nest if it starts to rain, at least during the daytime. An adult will also stand over the eggs during the heat of the day. Based on six night checks it appears that adults do not attend incomplete clutches at night.

Incubation begins once the clutch is complete and the attending adult spends more and more time at the nest as incubation proceeds (Fig. 3). During the daylight hours, adults spent an overall average of 42.3% of the time on the nest in 1969, 57.8% in 1971. These figures are low when compared to other species of Charadriidae, since in most species both sexes share incubation and eggs are usually not left unattended for long periods.

The increased attentiveness in 1971, as compared to 1969, may have been related to warmer temperatures, since adults spend the highest percentage of the time on their nests during the hottest period of the day (Fig. 4). The bird does not sit on the eggs during these hot periods, but merely stands over them to provide shade. When standing over the eggs the feathers on the head and back are raised, the eggs are exposed to the air but shaded, and the bird pants. Maclean (1967) described a similar posture in the Double-banded Courser and noted that it faces away from the sun during warm periods. The Mountain Plover also tends to face away from the sun during the heat of the day (Table 2).

Night observations during the incubation phase showed an adult on the nest on 22 of 27 occasions. On three checks at separate nests when the adult (marked) was not on the nest, I found the adult within 30 m of the nest. One of these adults was not on the nest at 22:30 one night, but was on at the same time the next night and I could detect no difference in weather conditions between the two nights. Two observations suggest that the preceding cases are the result of the birds periodically leaving the nests at night rather than merely being the result of the birds walking away from the nests as I approached:

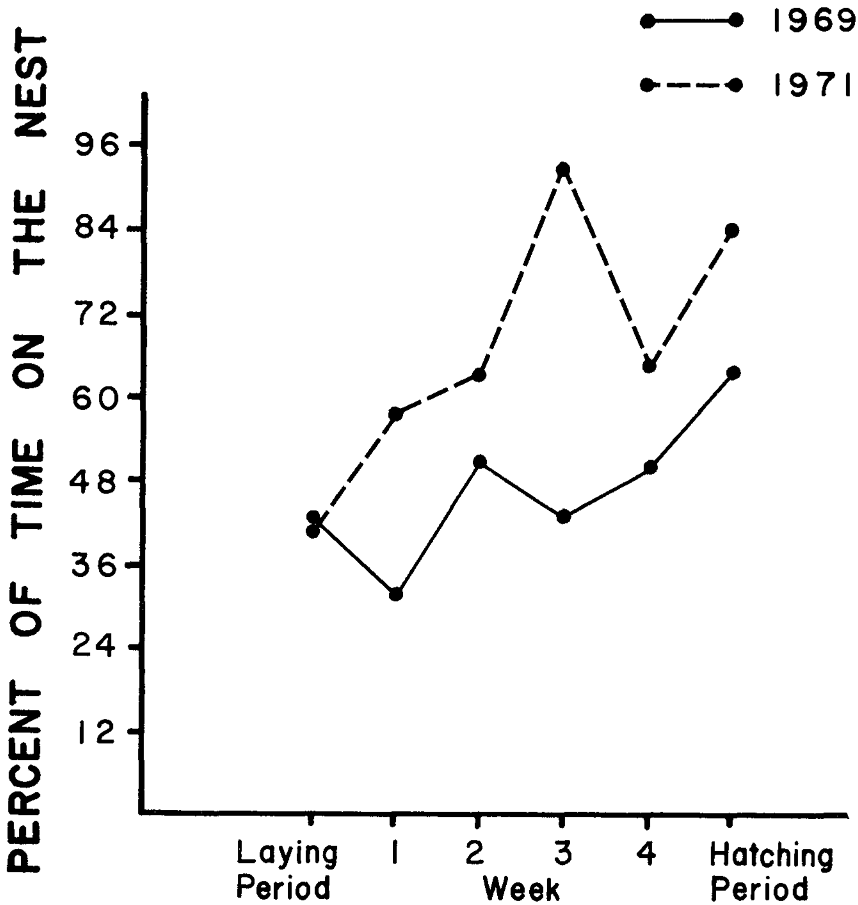

FIG. 3. Average percent of daylight hours spent on the nest by incubating adults vs. stage in incubation. Based on 727 checks of 55 nests in 1969 and 180 checks of 13 nests in 1971.

(1) when I checked birds on the nest at night with a spotlight, they either showed no signs of alarm or flew off the nest into the distance (2) in one case I purposely flushed a bird from the nest on an extremely dark night and 20 min later it was within 25 m of the nest.

Accumulation of nesting material.—When the first egg is laid there is usually no nest lining in the scrape, but the attending adult adds nest material throughout egg-laying and incubation. All sorts of objects lying near the nest may be added to the lining, certain items being more common than others. The main nesting material in 133 nests was: cow manure chips—66 nests,

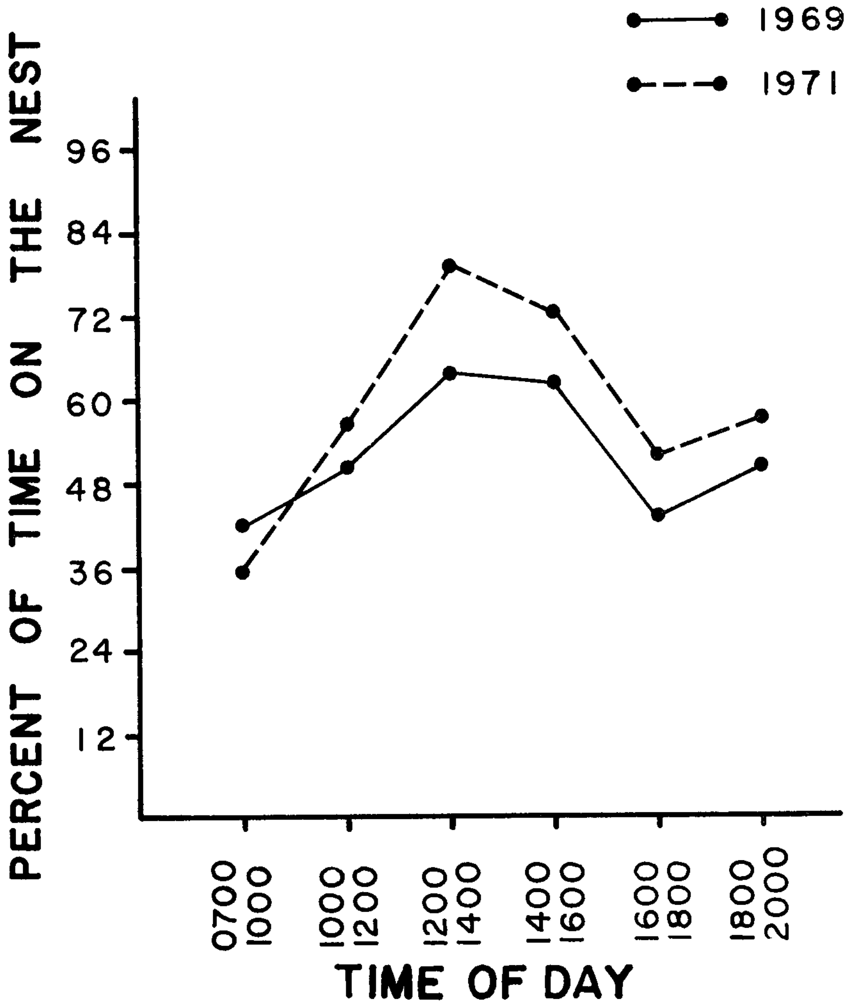

FIG. 4. Average percent of time spent on the nest by incubating adults vs. time of day (based on the visits cited in Fig. 3).

blue grama or buffalo grass rootlets—42 nests, blue grama or buffalo grass leaves—20 nests, and *Cymopterus acaulis* or *Lomatium orientale* seed pods—four nests. Less common items include rabbit manure, and two species of lichen (*Parmelia molliuscula* and *Nostoc* sp.). Although most items are lying on the ground near the nest, the birds will pull out rootlets and break chips from dried cow manure piles.

Response to human intruders at the nest.—The response of incubating

TABLE 2

ORIENTATION OF INCUBATING ADULTS TO THE SUN AT DIFFERENT AIR TEMPERATURES IN MAY, 1972*

	Temperature		
Orientation to Sun	16°C or Less	Greater Than 16°C Less Than 21°C	Greater Than 21°C
Facing Sun	4	4	1
Facing Away From Sun	4	14	26
Intermediate Positions	12	6	2

* These records were obtained as the temperature rose throughout the day on three cloudless days.

birds during the day to the approach of a human is variable. Frequently the bird will quietly leave the nest while the intruder is still 50–100 m away, but on some occasions it waits until the intruder is near the nest. If the intruder does not leave, the bird may move away even more, but it will usually stay in the vicinity of the nest and perform a variety of distraction displays, accompanied by several distinct vocalizations (Graul 1974).

The frequency and duration of the distraction behavior seem to increase as incubation progresses and peak at hatching time. Occasionally, a bird with an incomplete clutch will perform distraction behavior; this has also been noted for the Killdeer (*Charadrius vociferus*) (Hiett and Flickinger 1929).

Distraction displays have been interpreted as expressions of conflict between tendencies such as fleeing, attacking, and brooding (Simmons 1953, Lind 1961). One observation of a male Mountain Plover attending newly hatched chicks dramatically illustrates the intensity of the physiological stress involved. Initially the male was brooding the chicks, but as I approached it began performing distraction displays. As it was lying on the ground with wings extended it slowly lowered its head to the ground. Soon it became motionless; I picked it up and it was limp. Some birds have been reported to feign death in such situations (Armstrong 1965), but in this case the bird was dead. I could not be sure of the exact cause of death, but the pericardial cavity was filled with blood.

The response of incubating birds to the approach of a human at night is different than during the day. At night, the birds either remained on the nest with the spotlight on them or they flew from the nest. They never performed distraction displays.

Responses to other species.—Incubating birds will attack conspecifics, other small birds and thirteen-lined ground squirrels (*Spermophilus tridecemlineatus* when they get close to the nest (usually within 3–6m). In these situations the

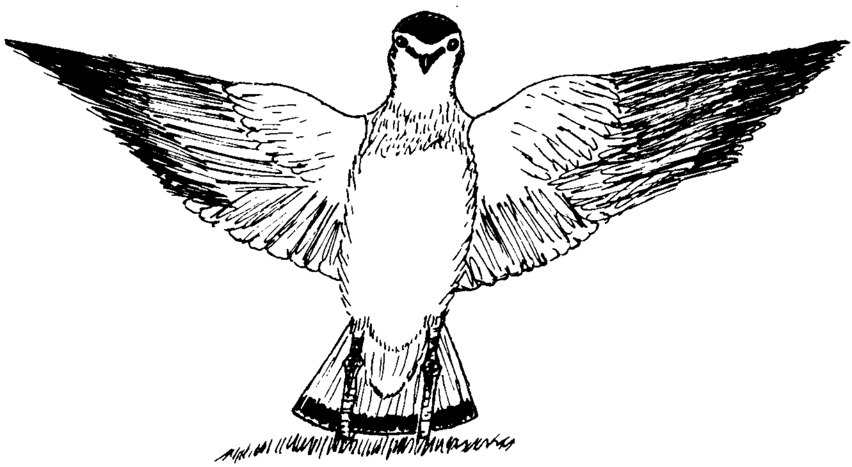

FIG. 5. Wings-out Rush Posture.

Mountain Plover, in the Wings-out Rush Posture (Fig. 5) moves quickly towards the intruder.

Cattle and other large mammals are generally tolerated until they approach within about one meter of a nest. If the large mammal gets closer the incubating bird will do one of two things: usually it will rush the intruder in the Wings-out Rush Posture, but one suddenly flushed directly towards an antelope (*Antilocapra americana*) and fluttered in front of its face. This latter behavior was also recorded by Walker (1955) in response to cattle and horses. Both reactions tended to deflect the intruders from the nest.

In 1974 I observed a kit fox (*Vulpes velox*) approach to within 5 m of an adult on a nest at dusk. The plover suddenly ran away while giving a loud series of *Ke-op* calls (Graul 1974). I scared the fox away and within 20 min the adult returned to the nest.

An incubating bird cocks its head every few minutes and looks upward. In fact, birds do this throughout the breeding season and I suspect that this behavior alerts them to the presence of potential aerial predators. When a potential aerial predator does approach a nest, the incubating bird crouches low on the nest with the head against the ground, as reported for the Double-banded Courser (Maclean 1967).

Egg losses.—In 1969, seven nests were abandoned because I removed the eggs (4) or tried to trap the adult at the nest (3); in 1971, two nests were abandoned because of my trapping attempts. These nests were not considered in determining hatching success and egg loss values. In 1969, 70% of the nests produced young; in 1971, 52.6% produced young (Table 3). The difference

TABLE 3

FATE OF NESTS IN 1969 AND 1971

Year	Total Nests	Hatched	Reasons for Losses: Human Disturbance[1]	Reasons for Losses: Weather[2]	Predation	Abandoned
1969	80	52	7	10	11	0
1971	21	10	2	0	3	6*

[1] Abandoned either because I removed the eggs or tried to trap the adult at the nest.
[2] Abandoned either because of hail damage to the eggs or because the nest was covered by water.
* In one nest all eggs were infertile. The cause of abandonment in the other nests was unknown.

in hatching success between the two years can be explained by the high desertion rate in June 1971. These figures compare favorably with the 56% hatching success listed by Lack (1954) for 24 precocial, ground-nesting species.

Weather can cause a heavy loss of nests on the shortgrass prairie. One hail storm, on 5 May 1969, damaged 20 of 72 eggs in 14 of 25 active nests. One adult Mountain Plover on a nest, a Horned Lark, and a Mourning Dove (*Zenaida macroura*) were found dead, apparently killed by the hail. Such storms are not uncommon in this area, but a given storm is usually fairly localized. Cody (1971) reported one hail storm near this area that killed hundreds of birds.

Following such storms, Mountain Plovers removed damaged eggs from their nests if there was a break in the shell with a protruding edge—eggs with slightly crushed spots were not removed. If two or more eggs were damaged badly, or if the nest was flooded, the adult usually abandoned the nest. One bird removed all three eggs that were damaged by hail, and then abandoned the nest.

I assumed that when eggs were missing from the nest during fair weather they were taken by predators and, on this basis, 15.1% of 73 nests in 1969 and 15.8% of 19 nests in 1971 were destroyed by predators. I once watched a thirteen-lined ground squirrel take an egg from a nest. In the earlier mentioned case of a kit fox approaching a nest, the eggs were gone the next morning. Other potential egg predators in the area include coyote (*Canis latrans*), striped skunk (*Mephitis mephitis*), badger (*Taxidea taxus*), prairie rattlesnake (*Crotalus viridis*), and bull snake (*Pituophis melanoleucus*). Creighton and Porter (1974) found that Western Meadowlarks (*Sturnella neglecta*) occasionally rob eggs from Horned Lark and Lark Bunting (*Calamospiza melanocorys*) nests on the shortgrass prairie, so perhaps they occasionally take a Mountain Plover egg. I rarely saw Crows

(*Corvus brachyrhynchos*) and Magpies (*Pica pica*) on my study area. Bailey and Niedrach (1933) speculated that a high percentage of Mountain Plover nests were lost as a result of cattle stepping on them, but I found no evidence of such damage.

At least some Mountain Plovers will renest if they lose their eggs. In two cases marked birds renested within two weeks of losing their nests.

Probably as a result of partial predation, hail damage, and because some females lay fewer than three eggs, the average number of eggs hatched per successful nest was 2.66.

Egg rotation during incubation.—In 1969 egg movement was recorded for 30 eggs throughout incubation (Fig. 6). The eggs were rotated considerably throughout incubation, apparently as a result of shuffling by the adult bird, but during hatching they maintained a relatively stable position, usually with the pipped area upward. A similar pattern has been reported for the Ringed Plover (*Charadrius hiaticula*) (Laven 1940), and the Killdeer (Pickwell 1925). In contrast, in the Herring Gull (*Larus argentatus*) (Drent 1967) and the Black-tailed Godwit (*Limosa limosa*) (Lind 1961) eggs seem to remain in a stable position throughout most of the incubation period. The reason for these species differences remains unclear.

HATCHING PHASE

Incubation period.—Based on 13 nests the average incubation period (time from laying of last egg until it hatched) was 29 days. One clutch hatched in 28 days; three took at least 31 days. Some males do not start incubating until several days after the clutch has been completed, since they are still courting females (Graul 1973b)—this may explain the three long incubation periods.

Hatching of eggs.—The first slight crack commonly appeared on the eggs three to four days prior to hatching; a hole usually did not develop until about 12 hours before the chick emerged. After the first cracks appeared new cracks developed clockwise around the blunt end of the egg (with the pointed end towards the observer). Hatching actually occurred as the chick pushed the shell cap away from the rest of the shell. Peeping noises (Graul 1974) could be heard in the eggs up to three days before hatching.

Hatching intervals.—At 25 nests, all three eggs hatched within three hours (14 cases), eight hours (6 cases), ten hours (2 cases), 17 hours (1 case), 41 hours (1 case). Hatching, therefore, was usually synchronous, but in some cases there were considerable delays.

Egg shell removal.—Adults remove egg shells, but not always promptly as eggs hatch. In four instances where I flushed a bird from the nest during hatching it immediately removed the egg shells upon returning. The

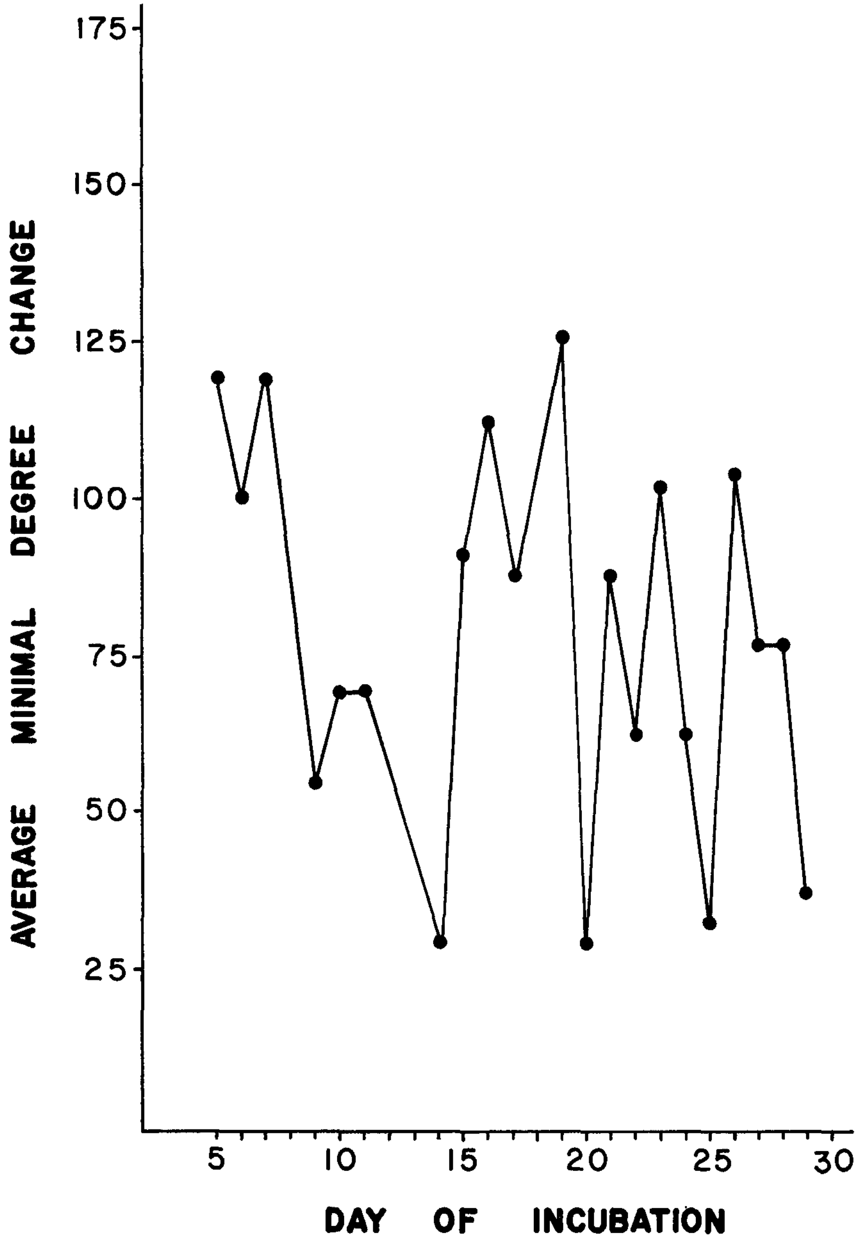

FIG. 6. The average minimal number of degrees that eggs are rotated with respect to the last nest check as a function of the stage of incubation. Based on 128 checks of 30 eggs.

Nethersole-Thompsons (1942) reported that Greenshanks (*Tringa nebularia*) and Dotterels also sometimes sit on empty shells for long periods before removing them.

Adult Mountain Plovers remove shells by grasping them in the bill and running 20–50 m before dropping them. Although the Black-fronted Dotterel (*Charadrius melanops*) (Littlejohns 1932), Kittlitz's sandplover (*Charadrius pecuarius*) (Conway and Bell 1968), and Kentish Plover (Hobbs 1972) also run away with egg shells, based on my own experience with shorebirds and numerous reports in the literature it seems that most shorebird species fly away with egg shells.

Prolonged incubation.—Occasionally one egg failed to hatch and was left in the nest when the adult moved away with the chicks. In one nest all three eggs failed to hatch and the adult, a female, maintained normal incubation for at least 43 days before finally abandoning.

CHICK PHASE

Departure from the nest.—Chicks are generally completely dry within three hours of hatching. If the last chick hatches in the morning or early afternoon and the weather is favorable, the entire brood is likely to leave the nest within three hours (8 of 10 cases). If the last chick hatches in late afternoon the brood is likely to stay in the nest until the following morning (4 cases). In rainy or cool weather (temperature under about 10°C), the brood may stay in the nest for up to 24 hours (4 cases).

During the first day after hatching the adult broods the chicks for bouts of about 4–5 min about every 12–15 min. When not brooding, the adult frequently feeds 50–100 m from the chicks. By the time the chicks are a few days old, however, the adult often stays near them while feeding. In view of the frequent absences of the adult, I never saw mixing of broods among the 229 marked chicks.

Within the first 24 hours chicks slowly pick at various objects, and by the end of this period, they sometimes successfully catch small insects. The same timing has been reported for the Killdeer (Bunni 1959).

Daily behavior patterns.—For about the first two weeks chicks are brooded much of the time in the cool early morning hours. They then spend most of their time feeding until the heat of the day, when adults and chicks of all ages seek ways to avoid the heat. This is achieved by seeking shade and/or by keeping the body off the ground.

Chicks will seek shade under small weeds or cacti, and broods, with accompanying adults, frequently congregate where there are restricted patches of shade. Such aggregations are found, for example, on weedy patches around cow watering tanks, and in the shadows of fence posts and telephone poles.

When other sources of shade are lacking, chicks stand in the shadow of the adult. I have even seen this reponse in a nearly fledged chick.

Adults frequently shade their chicks while standing on old cow manure piles. This probably has two advantages in cooling—greater exposure to wind and lower temperature of the substrate. Six wind velocity readings taken at seven cm above the ground averaged 3.5 times the average velocity from six readings at ground level. As a crude measure of substrate temperature I measured surface temperature at noon on cow piles and on adjacent ground, while the general air temperature was 25°C. Keeping the thermometer in place for five minutes in the shade, records for 10 occasions averaged 43.5°C for the ground temperature and 37.5°C for the cow pile temperature. Once I found a chick that had crawled 30 cm up into a shrub. Again, the advantage gained was presumably related to the cooling effect of the wind.

Two observations illustrate the serious consequences for these chicks of extended exposure to the sun. On both occasions, chicks under five days old were confined with the temperature at 27°C while I tried to capture the adult. All six chicks were dead within 15 min. At cooler temperatures I often confined chicks without shade for 20–30 min with no ill effects.

Aggression between the chicks of a brood appeared early and was sometimes related to competition for shade. For example, if one chick is standing in a small patch of shade and another tries to share it, one will usually peck the other until it leaves.

Response to human intruders.—Whenever I approached an adult attending a newly-hatched brood, the adult usually responded with distraction behavior and calling (Graul 1974). At least in some cases, the chicks do not crouch and freeze promptly in response to the adult alarm calls, but they do freeze if the adult leaves the immediate area. As the chicks get older they run away at the approach of an intruder instead of crouching. This transition is gradual, but appears to take place at about 10–14 days of age. Corresponding with this change in chick behavior, attending adults gradually stop performing distraction displays; they give only alarm calls with large chicks.

Brood movements.—During the first three days after hatching most broods move steadily away from their nest sites (Fig. 7). Thereafter, most broods remain within 300 m of the nest until fledging time. Two broods, however, moved over 800 m in the first two days, directly to weedy areas near cow watering tanks.

Chick losses.—Mortality is highest in chicks less than three days of age and appears constant thereafter (Fig. 8). In 1971, 16 broods of nearly fledged chicks averaged 1.37 chicks per attending adult. This average indicates that not more than 56.5% of the hatched chicks reached fledging age. This

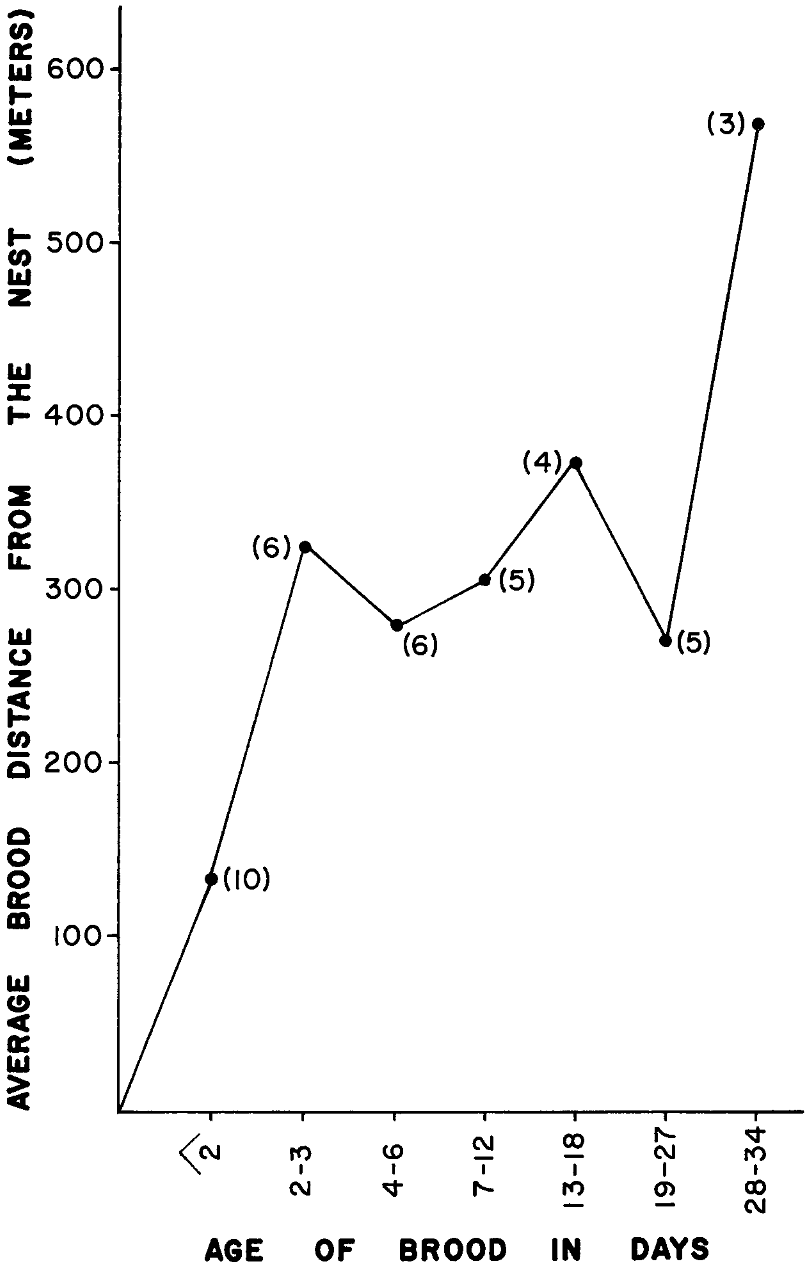

FIG. 7. The average distance broods move from their nests vs. age. Figures in parentheses represent number of broods sampled.

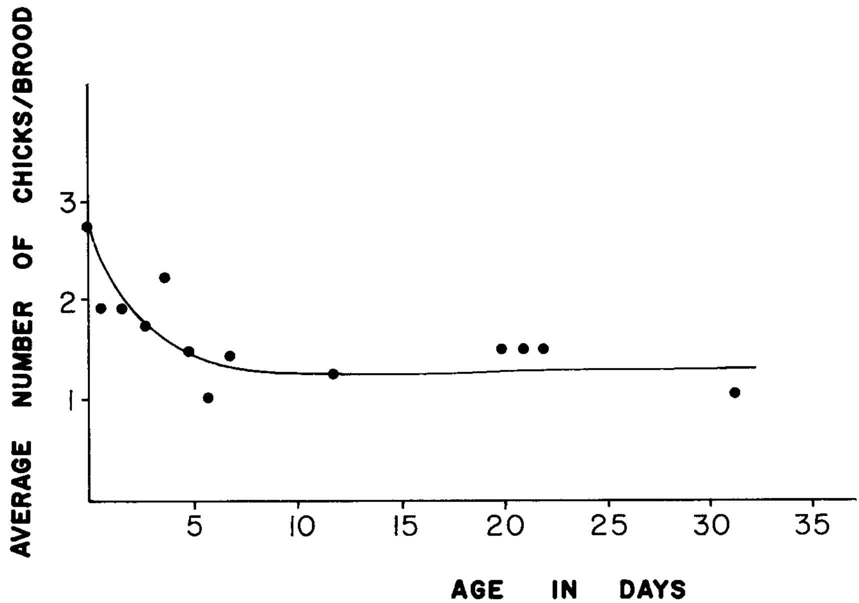

FIG. 8. The average number of chicks per brood vs. age of the chicks (N = 31), based on 1969 and 1971 data.

figure is probably high, since adults that had lost entire broods were excluded from the sample. These data agree with Laun's (1957) observations, since he rarely saw an adult with more than one large chick.

An independent estimate of fledging success was obtained by measuring the juvenile/adult ratio in flocks during the last two weeks of July. This lends support to the hatching success and fledging success for 1971. The ratio for 161 birds was one juvenile to three adults. By the end of July all chicks from nests started before 22 May should have been in these flocks and only 22.5% of the nests were started after this date. Since the success of these late nests was low, due to abandonment, I doubt that the ratio would have increased greatly; in fact, it may have decreased.

The causes of chick mortality are uncertain, but predation is no doubt partly responsible. R. Olendorff brought me the remains of one chick found in a Swainson's Hawk (*Buteo swainsoni*) nest and on one occasion I watched a Prairie Falcon (*Falco mexicanus*) take a small bird, but the prey could not be identified. One pair of Loggerhead Shrikes (*Lanius ludovicianus*) nested on my Keota study area and Sutton and Van Tyne (1937) reported that shrikes do occasionally take Mountain Plovers. An occasional Peregrine Falcon (*Falco peregrinus*) hunted on my study area, and coyotes and kit foxes are probable chick predators.

Some chicks may perish by not being able to keep up with the attending adult and other brood members. Once I saw a chick separated from its parent repeatedly attacked by another Mountain Plover adult that it had approached. Subsequently, the chick was attacked by a Horned Lark and probably would have been killed had I not rescued it.

Additional mortality may result from poor nutrition and/or disease, since I found a number of chicks that were poorly developed and underweight for their age. For instance, the average weight at six days of age was 15 g, but one six-day old chick weighed 11 g, equivalent to the average weight at hatching. In another instance, one 14-day old chick weighed 30 g, but its sibling weighed only 18 g. The small chick was still completely covered with down while its sibling had feathers on the spinal, humeral, and ventral tracts, and had some exposed primaries.

Chick fledging.—Bent (1929) described the newly hatched chick and Wetmore (1965) presented a colored photograph of one that still possessed the egg tooth. The apteria are black, a fact not mentioned in any previous description. Once the apteria are covered by feathers, however, the black coloration gradually fades and is not present in the adult.

Considerable variation exists in weights and measurements of chicks in each age class (W. Graul, in prep.), but fledging occurs at about 33–34 days of age, where fledging is defined as being able to fly at least 100 m. The fledging period is similar to that recorded for other plover species: Lapwing, 33 days; Dotterel, 31 days (Witherby et al. 1941); European Golden Plover (*Pluvialis apricaria*), 33 days (Bannerman 1961).

FALL FLOCK PHASE

In 1969, the first small flocks were observed in early July, but flocking began in mid-June, 1971. I watched the formation of these flocks in detail in 1971. As the heat of the afternoon increased, single birds would move about until they encountered others. This resulted in groups of up to four plovers resting in the shade near each other. As evening approached, however, aggression increased and birds would disperse to feed.

In both 1969 and 1971 the flocks gradually increased in size to an average of about 35 birds in late July. Two juveniles were seen in such flocks at distances of 1500 m and 3000 m from their hatching sites. In one case a flock was flushed and one marked juvenile (44 days old) stayed behind with an adult. The latter was presumably the parent, since it gave a series of alarm calls before both birds flew after the flock. Apparently not all families flock together, however, since on five occasions I have seen a fledged juvenile alone.

Flocks spend the heat of the day resting in shade, especially under weeds near cow tanks. When these flocks disperse to feed, low intensity aggressive encounters develop and at times the aggression seems to spread throughout the flock (Graul 1974).

Flocks continue to increase in size until mid-August. By this time they begin to leave the area and flocks can be seen flying in the wheeling, dipping, precision maneuvers typical of shorebirds. Flocks are still in the Weld Co. area in September, but these may represent birds from other breeding areas. Nancy Hurley estimated 2500 in a flock on 23 September 1972, but apparently this is an exceptionally late record (R. Ryder, pers. comm.).

Birds of the year can be distinguished easily from adults in these flocks. The body coloration of the young birds resembles the spring plumage of adults except that black crown and lore lines are absent, and instead their crowns have a finely striped appearance. Adults in these flocks are in the process of losing their black facial markings (this actually begins during nesting), and bright rusty colored feathers are appearing on the back.

DISCUSSION

In deserts and semi-arid areas species must cope with certain predominant features: aridity, heat, high solar radiation, irregular precipitation patterns, and sometimes strong wind conditions (Serventy 1971). Additionally, ground-nesting birds in all habitats must evolve special anti-predator adaptations, since they are particularly vulnerable to predation (Lack 1968). In the preceding sections various aspects of the Mountain Plover's breeding biology have been described and compared to other species. These comparisons will be used to argue that the semi-arid features of the shortgrass prairie have had a major impact on the evolution of the Mountain Plover.

Adaptations to climate.—The shortgrass prairie has a harsh climate, and apparently because of the high probability of severe weather in April and extremely hot, arid conditions in summer, the Mountain Plover laying period has been condensed to about a 60-day period. To maximize reproduction within this period these birds have evolved numerous mechanisms that reduce the effects of the aridity, heat and intense solar radiation. Of special importance are restriction of most activity to early morning and late evening periods, seeking shade during the heat of the day, and standing on cow manure piles. As in many desert birds, independence from free water is a fundamentally important adaptation (Fisher et al. 1972).

Shading by the adult during the heat of the day must be of vital importance in reducing effects of high temperatures and high solar radiation on both eggs and chicks. Olendorff (1972), for instance, reported that on the shortgrass prairie three young were produced at shaded Ferruginous Hawk (*Buteo regalis*) nests while only 1.71 were produced at unshaded nests, the difference attributable to addled eggs in the unshaded nests. Standing over eggs or chicks must produce heat problems for the adults, however, and these are eased by raising the dorsal feathers, panting, exposing the legs, and facing away from the sun. The latter behavior was noted by Maclean (1967) in the Double-banded Courser and has been discussed in detail for other species by Drent (1972).

Two physical characteristics of Mountain Plover eggs seem likely to be adaptations that reduce water loss at high temperatures and/or aid in heat retention at low temperatures: rounded egg (low surface to volume ratio), and thick egg shell. These adaptations may be especially important, since incubating adults spend so much time off nests. Being off the nests so much may, in turn, be necessary to allow the adults to feed for prolonged periods. This might be particularly important in the Mountain Plover, since I have argued elsewhere (Graul 1973b) that food supplies (insects) are sometimes extremely low on the shortgrass prairie.

The black skin of the chicks probably has evolved in response to the high solar radiation and/or the cool temperatures in early morning. Three possible explanations for the black coloration exists. Many desert animals possess black coloration (Schmidt-Nielson 1964) and black can be an efficient protective coloration in desert areas, since it allows an individual to blend into existing shadows (Serventy 1971). This interpretation, however, does not explain why the black is restricted to the apteria and why such altricial species as Mourning Dove and Yellow-billed Cuckoo (*Coccyzus americanus*) have black skin, since altricial chicks do not generally rely on protective coloration. It seems more likely that the black coloration might allow small chicks to absorb solar radiation during cool periods of the day (Heppner 1970; Lustick 1969, 1971; Ohmark and Lasiewski 1971). This again might be particularly important if food is sometimes a limiting factor on the shortgrass prairie. Alternatively, black skin might act as a shield against ultra-violet radiation (Porter 1967).

One mechanism has apparently evolved in response to the severe storms that sometimes produce heavy rains and hail: covering the eggs when it starts to rain. Nesting on flat areas may be an adaptation to heavy rains, since this would reduce the chances of a nest being subjected to heavy runoff, as suggested for the Three-banded Plover (Brown 1948).

Anti-predator adaptations.—Several features presumably have evolved to reduce the chances of predation in general: coloration of eggs and chicks (Cott 1966), coloration of the adult (Graul 1973a), egg shell removal (Tinbergen 1967, Nethersole-Thompson 1973) and removing damaged eggs, nest sites in open areas (Maclean 1967, Klomp 1954), and dispersed nesting (Tinbergen 1972). The tendency for nests to be placed near cow manure piles may serve a disruptive coloration function, or it may aid birds in relocating their nests. It is doubtful that other advantages would be incurred by nesting near cow piles; old piles probably do not produce an odor to mask the scent of the nest and they are not used as feeding sites.

The tendencies to attack any nest intruder that does not pose a threat to the attending adult (small birds, thirteen-lined ground squirrel, cattle, antelope), and to perform distraction displays or flee when the intruder could harm the adult (man, kit fox) seem particularly adaptive. The increase in distraction behavior as incubation progresses is to be expected, since the chances of the parent raising a new brood decrease as the season progresses (Drent 1967). After hatching selection has apparently favored distraction behavior decreasing as the ability of the chicks to protect themselves increases—simultaneously, small chicks freeze at the approach of a potential predator, but older ones run away.

SUMMARY

A marked population of Mountain Plovers was studied in northern Weld Co., Colorado during parts of the five breeding seasons of 1969–72 and 1974. Special attention was given to breeding adaptations in relation to the arid, shortgrass prairie habitat.

Nests were found on flat, open expanses of blue grama or buffalo grass, frequently near old cow manure piles. Nests were initiated in late April with egg-laying terminating in mid-June. Eggs are normally laid at 1–2 day intervals with some extreme delays (4 days) recorded. The normal clutch was three and eggs averaged 38.1 mm × 28.6 mm with an average weight of 15.6 g. The eggs have a relatively rounded shape and thick shell. The daily attentive period was relatively short and the incubation period averaged 29 days. Eggs are rotated during incubation, but not during hatching. Slight cracks appeared 3–4 days before hatching and noises were emitted by the hatching chicks.

Seventy percent of the nests in 1969 and 52.6% in 1971 produced young. Predation accounted for 15.1% of the egg losses in 1969 and 15.8% in 1971. Weather accounted for 13.7% of the losses in 1969, mainly a result of hail damage. Badly damaged eggs were removed as were egg shells at hatching time.

Adults perform distraction behavior during incubation and with chicks. One adult died as an apparent response to stress during a distraction display performance. Although adults performed distraction behavior in the presence of man, they frequently attacked other intruders.

Most chicks were raised within 300 m of the nest and mortality was highest within three days of hatching. Chicks fledged at 33–34 days, but not more

than 56.5% of the chicks reached the fledging stage in 1971. Flocking began in mid-summer and flocks began leaving in August.

Many characteristics of this species appear to have evolved in response to (1) high summer temperatures, intense solar radiation, and aridity, (2) sudden storms, (3) predators, (4) fluctuating food levels.

ACKNOWLEDGMENTS

My 1969–72 field work was supported by a National Institute of Health Training Grant (No. 2 T01 GM01779), a Chapman Fund Grant, and a Sigma Xi Grant-in-Aid, while I was a graduate student at the University of Minnesota. My 1974 work was funded by a Faculty Research Grant administered by the University of North Carolina–Charlotte. I am indebted to David Parmelee, who provided the initial encouragement for this research; Frank McKinney, who offered guidance throughout; and Scott Derrickson, who commented on the manuscript. Ronald Ryder kindly made numerous facilities available to me at Colorado State University and many personnel at the International Biological Program's Pawnee Site helped me in various ways.

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