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REPRODUCTION AND NEST SITE CHARACTERISTICS OF AMERICAN COOTS AT DIFFERENT ALTITUDES IN COLORADO

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ABSTRACT.—Reproduction and habitat use of American Coots (*Fulica americana*) were investigated on four study areas in the major elevational areas of Colorado, one in the eastern plains, two in the high mountain valleys, and one west of the Continental Divide. Nests were started from mid-April to mid-July; peak initiation dates ranged from 25 April to 12 June. Coots at high elevations had a shortened territory establishment-to-nest initiation period. Eggs hatched from mid-May through early August with peak hatching from 30 May to 4 July. We found 354 nests, and eggs in 284 nests hatched. Nesting and hatching success, respectively, ranged from 68.6 to 84.9% and 85.2 to 92.4%, with more nest failures and eggs lost per nest than expected at the high altitude areas. Average clutch size was lower at high altitude and decreased at all elevations as the season progressed. Predators caused most nest (64.3%) and egg (45.9%) loss. All nests were over water and most (99.7%) were in cattail (*Typha* spp.) or tule bulrush (*Scirpus acutus*). Early-nesting coots (75.6%) used dead, remaining vegetation for nest cover; later nesters used live cover as it became available. Measurements of nest site vegetation height, concealment, water depth, and distance to open water were variable and depended on local conditions. Breeding densities ranged from 10.2 to 33.1 successful nests/ha of cattail and bulrush and were independent of altitude. Intermingling of open water and emergent cover influenced the number of nesting coots.

Few comparisons exist of the reproductive biology of an avian species breeding at different altitudes. The breeding of American Coots (*Fulica americana*) has been described at low and medium elevations (<1,680 m) in North America (Gullion 1954, Fredrickson 1970), but no studies have examined breeding parameters at high altitude (>1,680 m). The widespread distribution of coots and the steep elevational gradient in Colorado provide an opportunity to compare breeding at different altitudes. We studied coots in 1977–1978 on four marshes in Colorado in order to describe aspects of reproduction, compare areas, compare coots with other species, and gain insight on how altitude may influence the reproduction of birds.

STUDY AREAS AND METHODS

We selected four study areas to represent the major physiographic and coot breeding areas in Colorado (Fig. 1). Each area consisted of an emergent marsh of cattails (*Typha* spp.) and/or tule bulrush (*Scirpus acutus*) and areas of open water. The Plains site (16.7 ha, 1,446 m) near LaSalle, Weld County, and the Western site (24.4 ha, 1,634 m) in Brown's Park National Wildlife Refuge, Moffat County, were medium-altitude areas (840–1,680 m). In January–June, 1978, 4.3 ha of emergent vegetation was removed from the Plains site by drawdown, dragline, and bulldozer. The Mountain Valley site (14.4 ha, 2,425 m) near Buena Vista, Chaffee County, and the Mountain Park site (18.1 ha, 2,500 m) in North Park near Walden, Jackson County, were high-altitude areas. The term "park" refers to a large intermountain depression devoid of extensive forest. The Western and Mountain Valley sites were characterized by well interspersed emergent vegetation and open water.

We searched for nests at approximately weekly intervals on all study areas by wading or boating through emergent vegetation. Any platform with one or more eggs was classified a nest. If discovered after hatching, a platform was considered a successful nest if small shell fragments were present (Fredrickson 1977). Once found, nests were revisited every 7–11 days until hatching. For each nest we recorded type of cover vegetation, its condition (dead or alive), height of a representative sample of the vegetation, nest concealment (nest concealed on one, two, three, or four sides, and/or from above), water depth, and distance to open water.

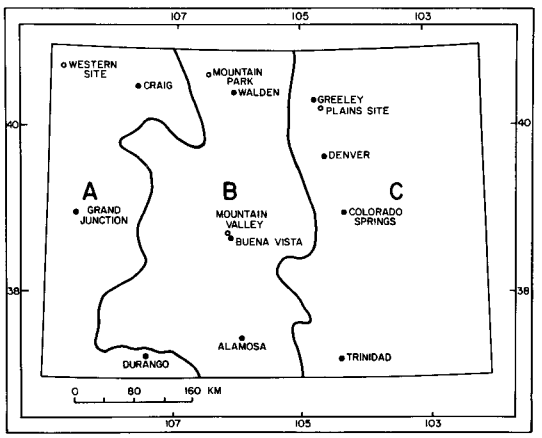

FIGURE 1. Physiographic zones of Colorado (modified from Fenneman 1931) and study area locations. A = Western, B = Mountain, C = Plains. Elevation range and major vegetation types: A. 1,525–3,050 m, pinon-juniper (*Pinus edulis* and *Juniperus* spp.), sagebrush (*Artemisia* spp.) and greasewood (*Sarcobatus vermiculatus*); B. 1,830–4,270 m, sagebrush, coniferous forest (*Pinus, Picea* and *Abies* spp.), and alpine (sedges, grasses, and *Salix* spp.); C. 1,040–1,830 m, shortgrass prairie (*Bouteloua* and *Buchloe* spp.) and sand sagebrush (*Artemisia filifolia*).

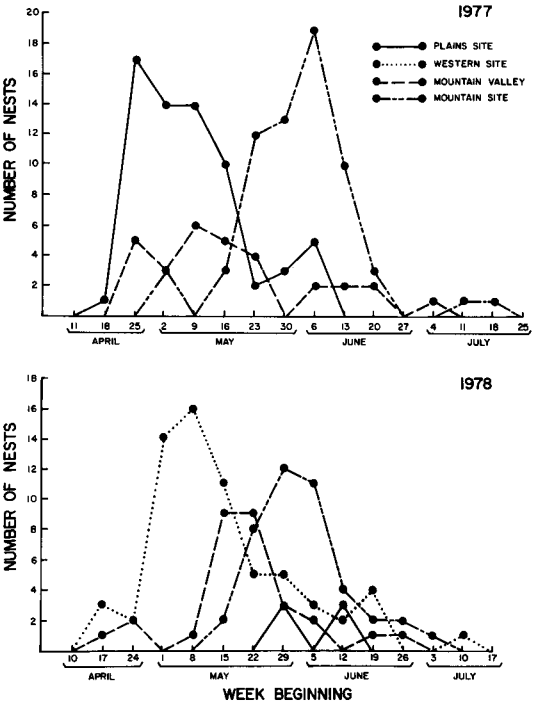

FIGURE 2. Number of coot nests initiated per week, four study areas, Colorado, 1977 and 1978.

Initiation dates of nests found during laying were calculated by backdating, assuming one egg laid per day (Gullion 1954, Fredrickson 1977). For nests found after laying, initiation dates were based on hatch dates, assuming a 23-day incubation period and one egg laid per day. Hatch was defined as the time at which all eggs had hatched. Nesting and hatching success calculations follow Mayfield (1975) and Johnson (1979). Breeding densities were estimated from the number of successful nests per hectare of emergent vegetation and for each emergent vegetation component.

RESULTS

NESTING CHRONOLOGY

Coots were not resident on the study areas, therefore displays such as patrolling, charging, splattering, fighting, and paired display (Gullion 1952) indicated the onset of territorial and breeding activities. Although coots arrived earlier (Gorenzel et al. 1981a) and territorial displays first occurred at lower elevations, the range of time between first displays and the appearance of first nests indicated a shortened period from territory establishment until nest initiation at high altitudes. This period was 4–5 weeks at the Plains and Western sites, but only 1.5–3 weeks at Mountain Park and 2.5 weeks at Mountain Valley.

Coots began nests from mid-April to mid-July (Fig. 2). Although the Western site was selected as a study area too late in 1977 to determine initiation dates, and low water levels at the Plains site delayed nesting six weeks in 1978, combined results indicate coots nested earlier at lower altitudes. The pattern of nesting at all altitudes was a low number of early nests followed within one to three weeks by an increase to peak numbers. Eggs hatched from mid-May to early August (Fig. 3). Hatching followed a pattern comparable to nesting, although it was influenced by differences in clutch size and the degree of nest failure.

NESTING SUCCESS

We found 354 nests, and eggs in 284 nests hatched; however, following the Mayfield (1975) method, nests visited only once (2 at Plains site, 22 at Western site) were excluded from nesting success calculations (Table 1). For the Mountain Park in particular and the high-altitude areas combined, there were more nest failures than expected over the entire nesting season ($P < 0.05$) and for nests initiated before or during the peak week of nest initiation ($P < 0.01$). Nests started after the peak week of nest initiation were more successful than expected ($P < 0.001$) at the medium-altitude areas.

Average clutch size was less at the Mountain Valley site than the other areas ($P < 0.05$) and was lower at the high-altitude areas ($P < 0.0025$). Modal clutch size was 8 eggs at

the Mountain Valley and 9 eggs at all other areas. For high-altitude areas combined, 90% of the nests contained 5–11 eggs and modal clutch size was 8 compared to a modal clutch size of 9 and 90% of the nests with 6–12 eggs at the medium altitude areas. Pooled clutch size data from all areas showed that weekly average clutch size decreased from a high of 9.8 eggs early in the season to a low of 5.0 late in the season. Multiple range tests indicated that means from weeks 1–5 were larger ($P < 0.05$) than all means for weeks 6–13. A similar trend was found at each study area and different altitude ($P < 0.05$).

Avian and mammalian predators were the primary causes of nest failure and egg loss (Tables 2 and 3). Suspected predators included raccoons (*Procyon lotor*), Black-billed Magpies (*Pica pica*), Common Crows (*Corvus brachyrhynchos*), and Black-crowned Night Herons (*Nycticorax nycticorax*). We found no difference ($P < 0.05$) in the expected and observed predation on nests or eggs between study areas or differing altitudes. Predation varied noticeably between years, especially at the Mountain Park site, with 23 of the unsuccessful nests (88.5%) and 98 eggs (58.3%) lost to predators in 1977, but only 3 nests (30.0%) and 18 eggs (28.1%) were lost in 1978. For all causes of egg loss combined, more eggs were lost per successful nest at the Mountain Park ($P < 0.001$) and the high-altitude areas ($P < 0.005$).

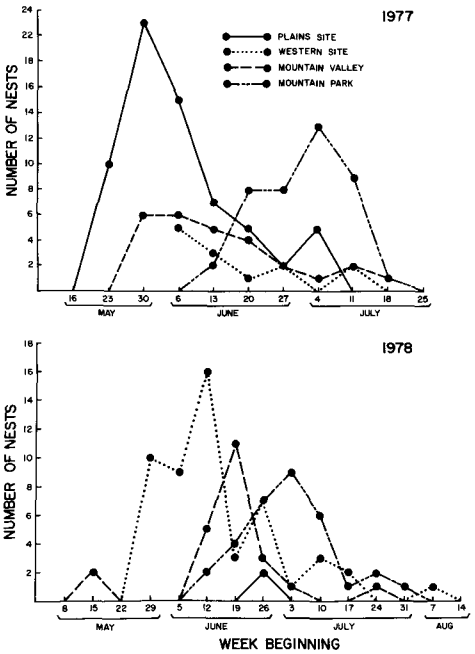

FIGURE 3. Number of coot nests hatching per week, four study areas, Colorado, 1977 and 1978.

NEST SITE CHARACTERISTICS

All nests were over water and most (99.7%) were in cattail or bulrush. Most nests (75.7%) were in bulrush, but bulrush covered nearly twice the area of cattail. One nest at Mountain Valley was in *Carex* spp. Dead or persistent vegetation was heavily used by early nesters (75.6%) for the first three to six weeks of the nesting season. Thereafter they changed to live cover. Examination of nest cover type in relation to date of nest initiation on areas with nearly equal proportions of cattail and bulrush indicated that 88.9% of the early nests at the Plains site and 40.7% of the early nests at Mountain Valley in 1977 were in cattails. After the peak of nest initiation, cover preference became less distinct at the Plains site, with 54.2% of the nests in cattail. The opposite occurred at Mountain Valley, with 65.6% of the nests in bulrush after the peak, and only 28.1% in cattails.

To illustrate conditions at the time of nest initiation, we excluded nests found late in in-

TABLE 1. Coot production data, Colorado, 1977–1978.

Production statistic	Plains	Western	Mountain Valley	Mountain Park	Total all areas
Number of nests	81	81	59	109	330
Successful nests	69	69	50	73	261
Nesting success, %	84.9	84.0	84.6	68.6	78.9
(95% confidence interval)	77.2–93.3	75.9–92.9	75.7–94.6	60.5–77.8	74.5–83.5
Number of eggs[a]	562	549	373	603	2,087
Clutch size					
Average[b]	8.6 ± 2.3	8.8 ± 2.3	7.5 ± 2.2	8.3 ± 1.2	8.4 ± 2.0
Range	3–14	5–13	2–14	4–16	2–16
Number of unhatched eggs[c]	32	53	26	89	206
Hatching success, %	92.4	88.6	91.5	85.2	89.0

[a] Number of eggs based on successful nests of known size: Plains, 65; Western, 62; Mountain Valley, 60; Mountain Park, 73.
[b] $\bar{x} \pm 1$ SD.
[c] Number of unhatched eggs from successful nests of known size.

TABLE 2. Fate of coot nests on four study areas, Colorado, 1977–1978.

Nest fate	Number of nests				
	Plains	Western	Mountain Valley	Mountain Park	Totals
Successful	71	90	50	73	284
Unsuccessful	12	13	9	36	70
Lost to predators	6	9	4	26	45
Avian	0	2	4	4	10
Mammalian	2	1	0	1	4
Unknown	4	6	0	21	31
Deserted	2	1	1	5	9
Unknown or other failure	4	3	4	5	16
Total nests	83	103	59	109	354

cubation or after hatching. Average height of vegetation at the nest was: Plains site, 63 cm; Western site, 80 cm; Mountain Valley, 75 cm; and Mountain Park, 36 cm. Average depth of water and range of depths at the nest were: Plains site, 69 cm, 24–142 cm; Western site, 41 cm, 21–64 cm; Mountain Valley, 37 cm, 2–101 cm; and Mountain Park, 50 cm, 0.5–119 cm. Average distance of the nest from open water and range of distances were: Plains site, 7.7 m, 0.3–35.1 m; Western site, 3.7 m, 0–22.9 m; Mountain Valley, 2.8 m, 0.3–18.3 m; and Mountain Park, 4.1 m, 0–22.9 m.

The majority of nests (77.9%) on all areas except Mountain Park were in what we considered good cover (concealed on three or four sides, or two, three, or four sides and from above). Conversely, 65.1% of all nests at Mountain Park were in poor cover. As incubation progressed, nests became better concealed owing to new growth and the tendency of coots to pull green shoots over the nest forming a canopy. Forty percent (39.7%) of all nests had at least a few shoots pulled over them.

Many nests at Mountain Park were in shallow water and/or had poor cover. These factors may have allowed better nest visibility and accessibility to predators and contributed to the high nest failure at this site. There was no difference ($P < 0.05$) in average water depth at successful vs. unsuccessful nests, nor any relationship ($P > 0.05$) between water depth class and nest success in 1977, when predation was the major cause of nest failure. Cover and nest success were related ($P < 0.05$), but the results were the opposite of those expected, nest success being positively related to poor cover.

BREEDING DENSITIES

Breeding densities (Table 4) were based on total area of emergent plants including species that were infrequently or not used for nesting, i.e., sedges (*Carex* spp.), spike rush (*Eleocharis macrostachya*), salt grass (*Distichlis stricta*),

TABLE 3. Fate of coot eggs on four study areas, Colorado, 1977–1978.

Egg fate	Number of eggs				
	Plains	Western	Mountain Valley	Mountain Park	Totals
Hatched	530	496	347	514	1,887
Lost to predators	35	61	20	116	232
Avian	0	9	20	20	49
Mammalian	16	13	0	3	32
Unknown	19	39	0	93	151
Deserted	13	26	15	60	114
Dead embryo	2	0	0	1	3
Buried in nest	1	6	0	5	12
In water	11	6	11	22	50
Broken	1	0	2	4	7
Unknown or other loss	19	29	15	24	87
Total eggs lost	82	128	63	232	505
Total eggs laid	612	624	410	746	2,392
Eggs lost/successful nest	0.49	0.86	0.52	1.22	0.80

[a] Eggs from successful and unsuccessful nests for all years except the Western site 1977; successful nests of known size only.

TABLE 4. Breeding densities of coots as number of successful nests/ha of emergent vegetation habitat on four study areas, Colorado, 1977–1978.

Cover type	Plains	Western	Mountain Valley	Mountain Park
Total emergent vegetation	9.6/0.7/7.0[a]	10.7/17.4/14.0	30.0/25.6/27.8	14.8/11.6/13.2
Carex spp.	0/0/0	0/0/0	16.7/0/8.3	0/0/0
Scirpus spp.	16.5/0/11.2	16.0/28.7/22.0	47.0/41.2/44.1	14.8/11.6/13.2
Typha spp.	13.6/1.3/9.9	75.0/50.0/62.5	22.5/22.5/22.5	0/0/0
Combined *Scirpus* and *Typha* spp.	15.4/1.0/10.2	17.1/29.2/22.8	35.1/31.1/33.1	14.8/11.6/13.2

[a] 1977 breeding density/1978 breeding density/combined 1977–1978 breeding density based on available habitat.

common reed (*Phragmites communis*), and common three-square (*Scirpus americanus*). A better estimate based on the common robust emergents, *Typha* spp. and *Scirpus acutus*, ranged from a low of 1.0 successful nests/ha at the Plains site in 1978 to a high of 35.1 at Mountain Valley. The 1978 estimate at the Plains site was not representative of normal conditions and indicated the importance of water and habitat conditions (Gorenzel et al. 1981b). The 1977 density estimates at the Western site were low owing to the late date of nest search. Assuming that the 1977 Plains site and 1978 Western site estimates represented normal conditions for the study period, multiple range tests indicated that the Mountain Valley and Western site estimates were greater than the other areas and different from each other ($P < 0.05$). High- vs. medium-altitude breeding densities did not differ ($P > 0.05$).

DISCUSSION

Altitude, through climate, influenced the timing of nesting events. The arrival and subsequent nesting of coots depended on ice thaw at the high-altitude areas, particularly at Mountain Park where ice did not melt until early April (Gorenzel et al. 1981a). The medium-altitude areas had earlier nest initiation and peak hatching dates compared to the high-altitude areas. Similar timing has been reported for other species. Meadow Pipits (*Anthus pratensis*) in Great Britain bred one day later for every 40 m rise in altitude (Coulson 1956). Song Sparrows (*Melospiza melodia*) in the Sierra Nevada bred three days later for each 100–125 m rise up to 2,000 m elevation (Johnston 1954). Morton (1976, 1978) documented that snowpack influenced the date when egg laying began but not the date of first arrival of White-crowned Sparrows (*Zonotrichia leucophrys*) on their Sierra Nevada breeding grounds.

Coots at high altitudes had shorter periods from territory establishment to nest initiation. Telescoping of the timing of events suggests that either coots at high altitudes arrive in an advanced state of physiological readiness or some breeding events are time-compressible. One would expect birds breeding at high altitudes or latitudes to be adapted to a short breeding season. Water Pipits (*Anthus spinoletta*) at 3,200 m in Wyoming arrive physiologically ready to begin breeding (Verbeek 1970). High-elevation populations of White-crowned Sparrows exhibit more rapid nest building, onset of laying, and fledging compared to lower elevation populations (Morton 1976).

Coots at all altitudes showed a similar basic pattern of nesting with a low number of early nests increasing to a peak within one to three weeks, then decreasing with one or more lower peaks. Fredrickson (1970) suggested that a second peak represents renesting or late nesting of young birds. Younger coots nest later than older coots (Crawford 1980), indicating that the pattern of nesting is related to the age structure of the breeding population.

Clutch size of coots is affected by age; younger coots lay fewer eggs than older coots (Crawford 1980). Although coots at high altitudes in Colorado had smaller clutches, the data are influenced by the age composition of the population and survival rates of different age classes. These factors may differ between areas. Other proximate factors (reviewed by Klomp 1970) undoubtedly were important. Data from coot breeding studies in North America show no significant correlation between altitude and average clutch size ($P > 0.1$). Average clutch size at all Colorado sites decreased as the season advanced. Similar decreases have been noted in other studies (Gullion 1954, Ryder 1958, Fredrickson 1970).

Coots did not appear to prefer any particular plant species as nesting cover. Of more importance was the structure and location of the vegetation. Weller and Spatcher (1965) found that species of plant was irrelevant as long as it was standing in water and served to anchor the nest. Any apparent preference relates to what is available when coots begin nesting, i.e., the residual or over-winter vegetation. On the Colorado sites, cattails persist better than bul-

rush. Changes in plant use depend on the availability of new vegetation and on territorial behavior (Crawford 1980). Early-breeding coots establish a territory, nest in the available (dead) vegetation, and exclude later arrivals from nesting. New vegetation emerges later and is used by late nesters. Sugden (1979) reported that a shortage of nesting cover caused some pairs to delay nesting until it became available later.

The wide range in nest site measurements illustrates wide use of the emergent vegetation zone by coots and basic differences among the study areas. The poor nest concealment at Mountain Park was related to a lack of residual vegetation on portions of the study area. A shortened growing season due to the high altitude of Mountain Park also influenced nest concealment and the height of vegetation at the nest. Differences in water depth at the nest site were related to different bottom profiles and water regimes. Differences in the average distance to open water resulted from different patterns of vegetation growth. The Plains site, with the highest average distance to open water, had a wide emergent plant zone with little interspersion of open water. Mountain Valley, with the lowest average distance, had a narrow emergent zone with many emergent islands and channels of open water.

The relationship of nest success with poor cover at Mountain Park is explained by examination of the nesting habitat. Twenty-five of the 31 successful nests in poor cover were on two emergent "islands" located 30 m or more from the shore and surrounded by broad expanses of deep (>1 m), open water. Vegetation in these "islands" was exposed to wind, wave, and ice action, resulting in little carryover and concealment for the beginning of the breeding season. Nesting success was higher on these "islands" (74.0%), than elsewhere in the marsh (50.8%), probably owing to difficult access for mammalian predators. Increasing water depth deterred mammalian predation on marsh nests of Red-winged Blackbirds (*Agelaius phoeniceus*; Shipley 1979).

Breeding density, as calculated, depended in part on nesting success. The actual number of nesting pairs was related to interspersion of open water and emergent vegetation. Weller and Fredrickson (1973) noted the highest coot densities at a 50:50 cover : water ratio. Ryder (1961) showed that nest densities increased to over 400 nests/100 acres of available cover (9.9 nests/ha) as the proportion of open water to cover increased. We did not measure interspersion within the emergent zone but visually estimated that it was greatest at Mountain Valley and the Western site.

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