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REPRODUCTION AND NEST-SITE SELECTION BY WHITE-TAILED PTARMIGAN IN COLORADO

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White-tailed Ptarmigan (*Lagopus leucurus*) are widely distributed in alpine regions of western North America and are locally abundant in suitable habitats (Braun and Rogers 1971). Prior to 1966 little intensive research had been conducted on this species. Notable exceptions are the work of Weeden (1959) and Choate (1960, 1963). Most other references to the species provide limited information on distribution or some aspect of its natural history. Only 14 of 30 literature references of nests or clutches provide original data, and most describe only 1 or 2 nests.

Intensive research on the ecology of White-tailed Ptarmigan was initiated in Colorado in 1966. Results of these studies have been published in a series of papers (Braun and Rogers 1971; Braun and Schmidt 1971; May and Braun 1972; Stabler et al. 1974; Hoffman and Braun 1975, 1977; Braun et al. 1976). This paper summarizes data from 62 nests and hatch dates of 673 chicks observed during 12 years (1966–1977) of research on the southern White-tailed Ptarmigan (*L. l. altipetens*).

STUDY AREA AND METHODS

Nests were located at study areas in Colorado along the Front Range (Crown Point, Rocky Mountain National Park, Niwot Ridge, Loveland Pass, Guanella Pass, Mt. Evans), Collegiate Range (Independence Pass) and in the San Juan Mountains in southwestern Colorado (Mesa Seco) (Fig. 1). These areas have been described elsewhere (Braun 1969, Braun and Rogers 1971, May 1975, Braun et al. 1976).

Most nests were located by following hens. Two in 1968, and 1 in 1972 were located by radio telemetry. Several were found incidental to other activities, or reported to us.

Rock and vegetative cover were visually described and color photographs were taken for permanent records. Slope at nest-sites was measured with a clinometer except for a few instances when it was estimated. Elevation was determined from topographic maps. Eggs were measured with vernier calipers. Nests were checked at irregular intervals to determine their fates.

Field techniques are described by Braun and Rogers (1971). Timing of reproductive events was based on observations of marked birds and by back-dating age of chicks to estimate hatch dates (Giesen and Braun 1979a).

RESULTS

Chronology of nesting events.—Timing of White-tailed Ptarmigan breeding and nesting events in Colorado is controlled by climatic conditions (Braun and Rogers 1971). Adult males usually begin defending breeding territories in early to mid-April, with females arriving in late April or early

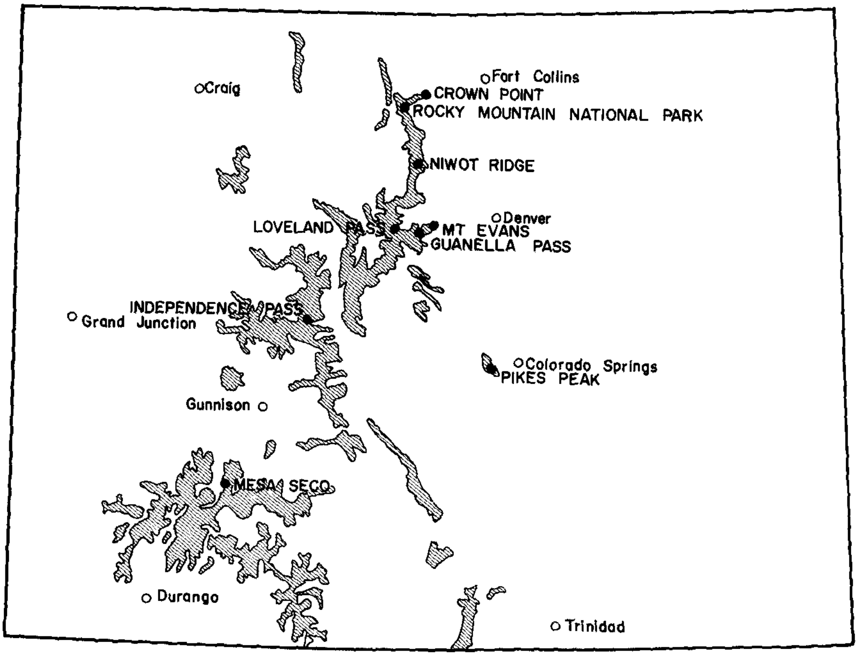

FIG. 1. Study areas (solid circles) and alpine habitats within Colorado.

May. In early years mated pairs are often seen in late April, while in normal or late years pairing begins in early to mid-May. Severe snowstorms may result in temporary separation of mated pairs as females retreat downslope to more protected areas (Schmidt 1969, Braun and Rogers 1971). Peters (1963) reported similar findings for Willow Ptarmigan (*Lagopus lagopus*) in Newfoundland.

Copulation and egg deposition began after females were in alternate (nuptial) plumage, usually in early June. Timing of prealternate (prenuptial) molt is controlled ultimately by day length (Host 1942) and appears to be further affected by amount of snow cover and resulting light intensity (Braun and Rogers 1971).

The temporal relationship between copulation and egg deposition is not known. Schmidt (1969) observed copulation in White-tailed Ptarmigan prior to egg deposition, but also observed 2 instances of copulation involving females that were apparently incubating. We assume that timing of copulation in White-tailed Ptarmigan is similar to that reported for Ruffed Grouse (*Bonasa umbellus*), approximately 3–7 days prior to egg deposition (Bump et al. 1947). Zwickel (1977) estimated a 4-day interval between copulation and laying for Blue Grouse (*Dendragapus obscurus*). White-tailed Ptarmigan are monogamous and the pair bond remains intact until late in incubation; thus copulation may occur several times before and during laying.

Timing of egg deposition was determined from intensive observations of 12 hens. These hens approached their nests for laying between 08:30 and 16:30 MDT. Hens deposited an egg soon after arriving at the nest, although they often remained on the nest for several hours, especially as clutches neared completion. There is no evidence that egg deposition occurred after dark.

The interval between deposition of successive eggs was estimated to be 26–30 h when eggs were laid on successive days. On some days no eggs were deposited. Three hens each laid 3 eggs in 4 days; another laid 4 eggs in 6 days. Hens deposited eggs later during the day on successive days and skipped every third or fourth day. Maxson (1977) observed a similar pattern in Ruffed Grouse.

Females spent increasing amounts of time on the nest as clutches approached completion, but incubation did not begin until the last egg was deposited. This differs from the report of Choate (1960) who reported incubation began 3 days (2 eggs) before clutch completion. We define incubation period as the interval between deposition of the last egg and hatching of the clutch (eggs within clutches usually hatched within a 2–6-h period). Incubation length was 23 days for 5 hens and 22–23 days for another. Pipping of eggs was observed 24–48 h prior to hatching.

In most years hatching did not begin until the first or second week in July (Fig. 2). The 12-year median hatch date was 15 July when varied from 6 July in 1977 to 23 July in both 1969 and 1973. Except for 1969 most of the hatch (>65%) occurred within a 2-week period. Zwickel (1977) reported a similar pattern of hatch for Blue Grouse on Vancouver Island. The long period of hatch in some years was the result of renesting (Giesen and Braun 1979c).

Peak of hatch varied predictably between areas within years. The hatch at Mesa Seco, Mt. Evans, Guanella Pass and Pikes Peak occurred 1–2 weeks earlier than at Rocky Mountain National Park. This may have been the result of different snowfall and solar radiation patterns as these areas were also earlier phenologically. Hatch dates at Crown Point and Independence Pass were similar to those in Rocky Mountain National Park.

Clutch-size.—Few clutches were located in any year so data for all years were pooled. Clutch-size varied from 2–8 eggs in 56 clutches examined. Four clutches were incomplete and 4 represented known renests. The remaining 48 clutches averaged 5.9 eggs (range 4–8). Reported clutch-sizes for 40 additional nests were found in the literature (Brewer 1874;

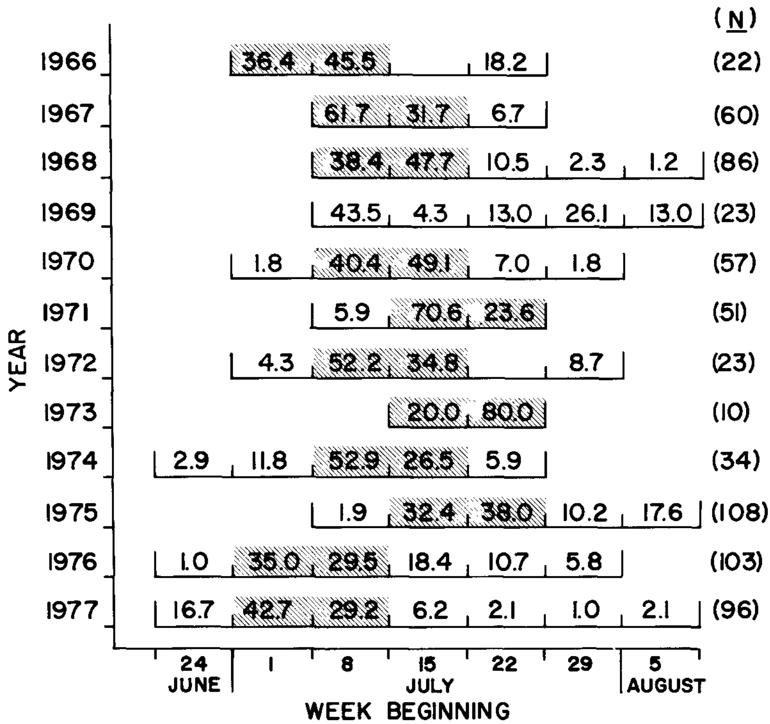

FIG. 2. Timing of White-tailed Ptarmigan hatching in Rocky Mountain National Park, 1966–1977. Percentage of chicks hatching in each weekly period is given for each year. Peak hatching periods are shaded. Sample sizes are in parentheses.

Lewis 1904; Sclater 1912; Bradbury 1915; Taylor 1920; Taylor and Shaw 1927; Weydemeyer 1931; Jewett et al. 1953; Thatcher 1954; Edwards 1957; Evans and Fisher 1958; Choate 1960, 1963; Bailey and Niedrach 1965). Clutch-sizes for these nests ranged from 2–8, excluding 1 of 9 eggs to which 2 hens contributed (Choate 1960). The average size of these clutches was 5.2 eggs. It is possible that some incomplete clutches, or renests, were among those reported. Clutches resulting from renesting have fewer eggs (Giesen and Braun 1979c). Other workers estimated clutch-size to range from 4–16 eggs (Bent 1932, Gabrielson and Lincoln 1959) and Batty (1874) reported that White-tailed Ptarmigan never lay more than 4 eggs.

We calculated average clutch-sizes separately for yearling (N = 17) and adult (N = 25) females. Those of adults were significantly ($P < 0.01$) larger than those of yearlings (6.2 vs 5.5 eggs). Clutch-size of yearlings ranged

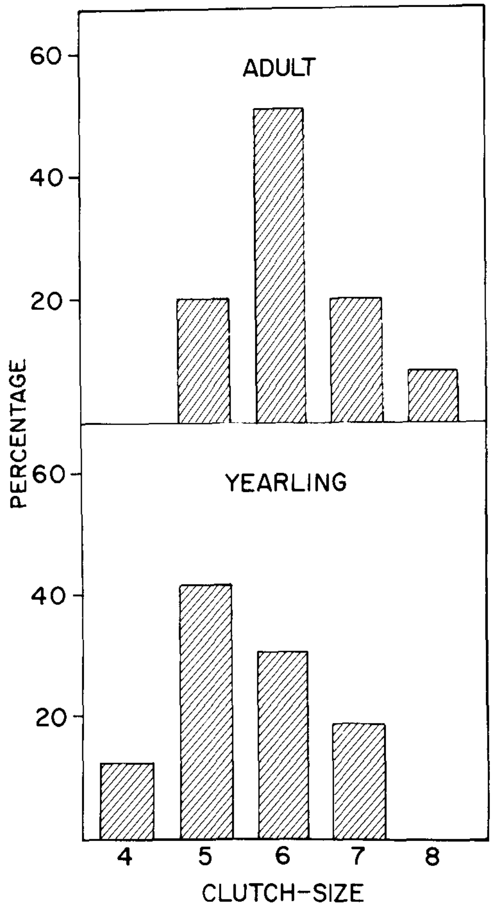

FIG. 3. Frequency distribution of clutch-size of yearling (N = 17) and adult (N = 25) female White-tailed Ptarmigan.

from 4–7, those of adults from 5–8 (Fig. 3). Zwickel (1975) described a similar relationship for Blue Grouse. Since the yearling to adult female ratio varies annually in White-tailed Ptarmigan, production of young is influenced by age structure of females in the population.

Egg size and coloration.—We examined 227 eggs for size and coloration between 1968 and 1977. These eggs represented 43 partial or complete clutches from 39 hens (eggs from 4 hens were sampled in 2 different years). Eggs were oval in appearance and averaged 43.74 ± 1.70 mm × 29.71 ±

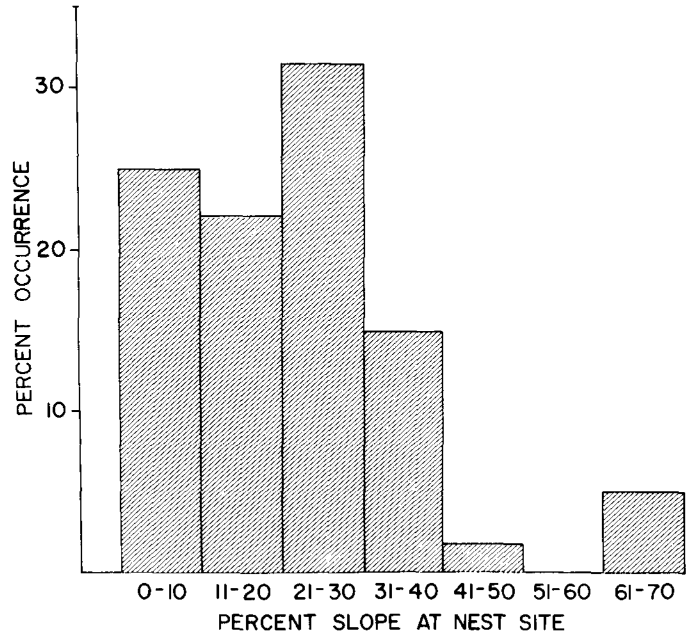

FIG. 4. Distribution of White-tailed Ptarmigan nest-sites (N = 60) by percent slope, 1966–1977.

0.68 mm ($\bar{x} \pm$ SD). Extreme measurements were 48.9 × 29.3 mm, 39.2 × 29.6 mm, 43.1 × 31.4 mm and 39.6 × 27.2 mm. Bent (1932) summarized measurements of 31 eggs, which likely included those reported by Bradbury (1915), Brewer (1874) and Sclater (1912). Choate (1960) reported measurements of 14 White-tailed Ptarmigan eggs from Montana. Measurements reported were within the range observed in this study.

Eggs were lightly to heavily blotched, or spotted reddish-brown on a creamy brown background. Blotches measured up to 6 mm in diameter, although most were less than 2 mm. Blotches on newly deposited eggs were deep red; those on eggs incubated for several days were dull reddish-brown. Fading of blotches has been reported for eggs of Willow Ptarmigan (Dement'ev and Gladkov 1952).

Nest-site characteristics.—Slope was measured at 60 of 62 nest-sites. The median was 20% ($\bar{x}$ = 21.4%) with a range from 0–70%. Slopes of less than 40% were selected by 93.3% (N = 56) of the nesting females, with nest-sites evenly distributed within this range (Fig. 4). Steep slopes were avoided, as only 4 nests were located on slopes over 40% and none was located on slopes over 70%.

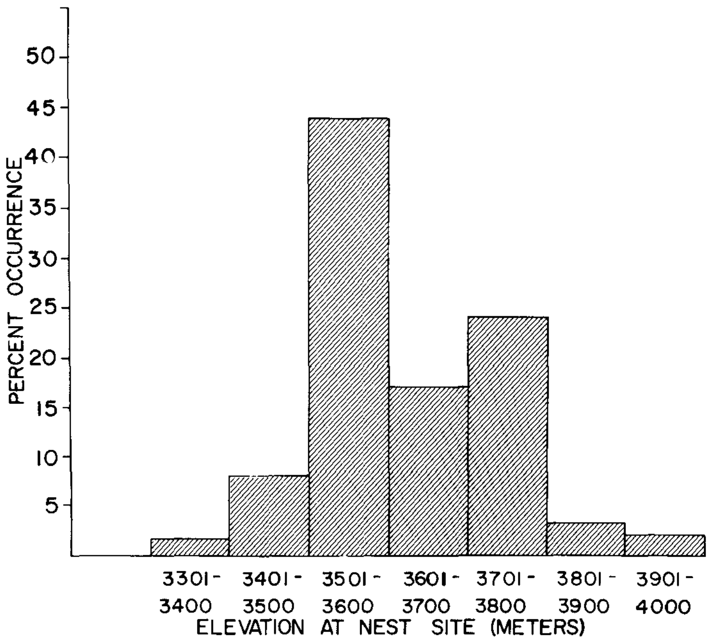

FIG. 5. Elevations of nests of White-tailed Ptarmigan (N = 59), 1966–1977.

Of 60 nest-sites examined, more (N = 19) were on south-facing than on north- (N = 15), west- (N = 14), or east-facing (N = 12) slopes. Chi-square analysis for preference of aspect indicated there was no selection. This was expected since hens nest within the territory of the male (Braun and Rogers 1971) and usually have limited choice of aspect. Although our searches for nests were not random, we did search territories at many locations within the study areas.

Nest-sites (N = 59) ranged in elevation from 3383–3901 m with a mean of 3618 m (median = 3597 m) (Fig. 5). Treeline depends on latitude, slope and aspect, and averaged about 3505 m on the study areas. Few nests (N = 7) were below treeline. Most were located in the krummholz, or within 250 m of treeline. Although some breeding territories extended to 3962 m, no nests were found this high. While this may reflect lack of search effort at these elevations, we believe most females nested on the lower periphery of their mate's territory.

Twenty-five of 62 nests (40.3%) were in rock or boulder fields, 20 (32.3%) in various turf situations, 11 (17.7%) in evergreen krummholz (usually *Picea engelmannii*) and 6 (9.7%) in willow (*Salix* spp.) krummholz. The importance of rocks was apparent as 12 of 20 nests in turf areas were near rocks or boulders.

Krummholz, both willow and spruce, served to protect incubating birds from the wind. In addition, the vegetation served to conceal the female. Most nests in krummholz were at the edge of a shrub clump or near an opening. This characteristic likely facilitated departure from the nest.

Five of 8 nests in turf situations were protected from wind by clumps or hummocks of sedge (*Carex* spp.) or grasses (*Deschampsia* spp. or *Poa* spp.). Two nests were in small natural depressions, possibly enlarged somewhat by the female. Only 1 of 62 nests had no obvious protection from the wind; it failed. Nest-sites described by Choate (1960) and Bent (1932) are similar to those described here. Lewis (1904) concluded, erroneously, that White-tailed Ptarmigan do not nest near willow. However, he searched primarily above the krummholz.

Based on our observations, suitable nesting sites are abundant on the alpine. This observation is supported by lack of reuse of old nest-sites, even when females returned to the same territories (Schmidt 1969, this study).

Nest construction.—Most nests were in natural depressions, which may have been slightly enlarged by the females. Average size of 38 nest bowls was 151 × 130 × 36 mm. Materials used in nest construction reflected the vegetation at the site, as materials were gathered within 40 cm. Depending upon site, dead leaves and stems of willow, spruce, grass or sedge were used. Lichens (principally *Dactylina madroporiformis*, *Thamnolia vermicularis* and *Cetaria* spp.) were commonly used as nesting material. Most nests contained several small white feathers.

Nesting success.—Success was determined for 60 of 62 nests. Thirty-four hens hatched all, or part of their clutches (56.7%). Only 2 nests were deserted, 1 after 30 days of incubation. Coyotes (*Canis latrans*) and weasels (*Mustela* spp.) were the primary predators, although 1 nest was depredated by corvids. Nests were not marked and observer interference was not thought to affect success, even though some were visited almost daily. Several nests in Rocky Mountain National Park, located near areas of high use by Park visitors, hatched. Yearly samples were too small to compare annual variation in success. Nesting success estimated from surveys of hens with and without broods was generally similar to that obtained from nest examination.

Hatchability of 177 eggs incubated to completion was 88.1% (156 of 177 eggs). All eggs hatched in 23 of 31 nests. Minimum egg fertility for 55 eggs from 10 successful nests in 1975 and 1976 was 94.5%. Of the 6 eggs that failed to hatch, 3 contained well developed embryos. The other 3 eggs were either infertile or failed to develop.

DISCUSSION

Timing of nesting is critical for avian species living in arctic-alpine environments. Climatic factors determine timing of resource availability and set the temporal boundaries within which a species mates, reproduces and rears young. White-tailed Ptarmigan in Colorado demonstrate behavioral and physiological adaptations for completing their reproductive cycle during the few months of favorable weather in summer.

Males acquire and defend territories prior to arrival of females (Schmidt 1969). Females return to their territory (and mate) of the previous year, eliminating the need for elaborate pair-formation and courtship displays. Territorial defense is entirely accomplished by males (Schmidt 1969) allowing females to devote their time to feeding. As a consequence, females have sufficient energy intake to undertake a prealternate molt and to complete ovarian development within 30 days. Of the North American Tetraonidae, White-tailed Ptarmigan have the smallest clutch-size (Johnsgard 1973), permitting a shorter egg-laying period.

Nests are located within the pair's territory, effectively limiting female choice of elevation and aspect. Within the territory females select snow-free nest-sites on areas of moderate slope. Depending on snow conditions, about 10–50% of the territory may be suitable for nesting.

Rock and vegetative cover is important for protection from inclement weather and less important as concealment. Although quantitative measurements of concealment and protection were not systematically recorded, detailed descriptions of nest-sites reveal most (61 of 62) were protected from the prevailing winds. Since females spend over 95% of the time on the nest during the incubation period (Giesen and Braun 1979b) it is energetically advantageous to have protection from the weather. In contrast, the concealment value of rocks and vegetation was judged to be of minor importance as most incubating females were exposed. The cryptic plumage of incubating females lessens visual detectability at least for human observers (Lewis 1904). Keppie and Herzog (1978) concluded that concealment from predators was more important than protection from weather in determining nest success of Spruce Grouse (*Canachites canadensis*).

SUMMARY

Nesting events of White-tailed Ptarmigan in Colorado began in early June after females completed their prealternate molt. Average clutch-size was 6.2 for adults and 5.5 for yearlings. Eggs were oval and averaged 43.74 × 29.71 mm in size. Incubation began after clutches were complete and lasted 23 days. Hatching usually occurred in mid-July, but varied annually due to spring weather. Predation by coyotes and weasels was the major cause of nest failure. Egg hatchability (88.1%) and fertility (94.5%) were high. Data from 62 nests indicated that most (93.3%) were on moderate slopes of less than 40% at elevations between 3501 and 3800 m. There was no selection for aspect. Nests were typically located adjacent to rocks or

boulders or in krummholz vegetation which protected them from the wind. Nests were usually shallow scrapes lined with dead vegetation collected at the nest-site.

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