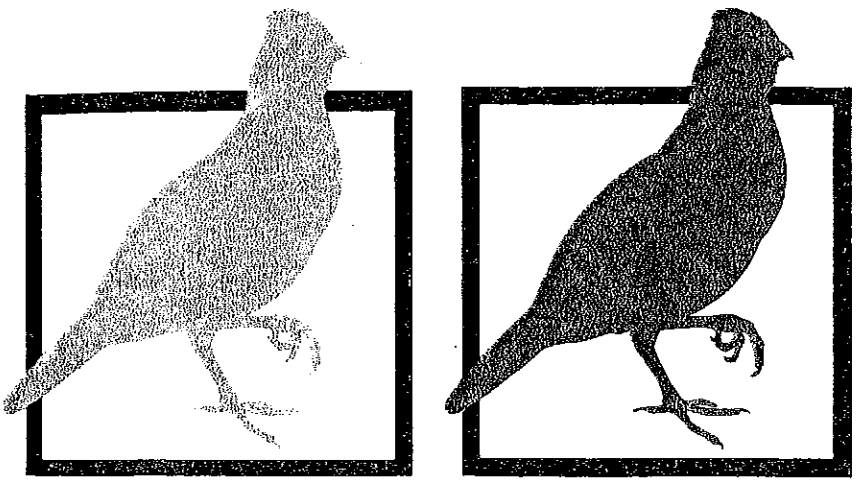
# Grouse and Quails of North America



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## TABLE 5
### ADULT WEIGHTS OF NORTH AMERICAN GROUSE

| *Species* | *Mean or Range of Means* | *Maximum Weight* | *References* |
|---|---|---|---|
| Sage grouse | | | |
| Male | 2010–2835 gm (71–100 oz.)* | 3175 gm (112 oz.) | Patterson, 1952 |
| Female | 1142–1531 gm (40–54 oz.)* | 1531 gm (54 oz.) | Patterson, 1952 |
| Blue grouse | | | |
| Male | 1150–1275 gm (14–45 oz.)* | 1425 gm (50 oz.) | Boag, 1965§ |
| Female | 850–900 gm (30–32 oz.)* | 1250 gm (44 oz.) | Boag, 1965§ |
| Spruce grouse | | | |
| Male | 501 gm (17.7 oz.) (14 birds) | 630 gm (22 oz.) | Stoneberg, 1967 |
| Female | 450–548 gm (16–19 oz.)* | 606 gm (21 oz.) | Stoneberg, 1967 |
| Willow ptarmigan | | | |
| Male | 535–696 gm (19–25 oz.)* | 804 gm (28 oz.) | Parmelee, Stephens, and Schmidt, 1967 |
| Female | 525–652 gm (19–23 oz.)* | 749 gm (26 oz.) | Irving, 1960 |
| Rock ptarmigan | | | |
| Male | 466–536 gm (16–19 oz.)* | 575 gm (21 oz.) | Irving, 1960 |
| Female | 427–515 gm (15–18 oz.)* | 550 gm (20 oz.) | Johnston, 1963 |
| White-tailed ptarmigan | | | |
| Male | 323 gm (11.4 oz.) (24 birds) | 430 gm (15.2 oz.) | Johnson & Lockner, 1968 |
| Female | 329 gm (11.5 oz.) (14 birds) | 490 gm (17.5 oz.) | G. Rogers (*in litt.*) |
| Ruffed grouse | | | |
| Male | 604–654 gm (21.5–23.3 oz.)* | 770 gm (27 oz.) | Nelson & Martin, 1953† |
| Female | 500–586 gm (17.9–20.9 oz.)* | 679 gm (24 oz.) | Bump et al. 1947 |
| Greater prairie chicken | | | |
| Male | 992 gm (35 oz.) (22 birds) | 1361 gm (48 oz.) | Nelson & Martin, 1953† |
| Female | 770 gm (29 oz.) (16 birds) | 1020 gm (36 oz.) | Nelson & Martin, 1953† |
| Attwater prairie chicken | | | |
| Male | 938 gm (33.1 oz.) (10 birds) | 1135 gm (40 oz.) | Lehmann, 1941 |
| Female | 731 gm (25.7 oz.) (6 birds) | 785 gm (28 oz.) | Lehmann, 1941 |
| Lesser prairie chicken | | | |
| Male | 780 gm (27.6 oz.) (20 birds) | 893 gm (31.5 oz.) | Lehmann, 1941 |
| Female | 722 gm (25.5 oz.) (5 birds) | 779 gm (27.5 oz.) | Lehmann, 1941‡ |
| Sharp-tailed grouse | | | |
| Male | 951 gm (33 oz.) (236 birds) | 1087 gm (43 oz.) | Nelson & Martin, 1953† |
| Female | 815 gm (29 oz.) (247 birds) | 997 gm (37 oz.) | Nelson & Martin, 1953† |

*Mean weights of these species vary considerably with season and/or locality.
†Reported as fractions of pounds by authors.
‡Reported as pounds and ounces by authors.
§Reported in graphic form, points interpolated.

TABLE 7

EGG CHARACTERISTICS AND INCUBATION PERIODS

| *Species* | *Spotting* | *Basic Color* | *Dimensions (mm)* | *Incubation (days)* | *References (for incubation)* |
|---|---|---|---|---|---|
| Sage grouse | Moderate | Buffy green or brown | 55 x 38 | 25–27 | Patterson, 1952 |
| Blue grouse | Moderate | Buff or pale brown | 48.5 x 35 | 24–25 | Godfrey, 1966 |
| Spruce grouse | Moderate | Buff or pale rust | 43 x 31 | 21 | Pendergast and Boag, 1971 |
| Willow ptarmigan | Heavy | White to pale brown | 43 x 31 | 21–22 | Westerkov, 1956 Jenkins et al., 1963 |
| Rock ptarmigan | Heavy | White to pale brown | 42 x 30 | 21 | Godfrey, 1966 |
| White-tailed ptarmigan | Moderate | White to reddish buff | 43 x 29.5 | 22–23 | Braun, 1969 |
| Ruffed grouse | Slight or none | Buffy white to cream | 38.5 x 30 | 24 | Bump et al., 1947 |
| Greater prairie chicken | Slight or none | White to olive buff | 43 x 32.5 | 24–25 | McEwen et al., 1969 |
| Lesser prairie chicken | Slight or none | White to buff | 42 x 32.5 | 25–26 | Coats, 1955 |
| Sharp-tailed grouse | Slight | Fawn to chocolate or olive | 43 x 32 | 24–25 | McEwen et al., 1969 |
| Bearded tree quail | None | Dirty white | 46.6 x 31 | 28–30 | this study |
| Barred quail | None | White | 30 x 23.7 | 22–23 | F. Strange, pers. comm. |
| Mountain quail | None | Pale buff to cream | 34.5 x 26.5 | 24–25 | F. Strange, pers. comm. |
| Scaled quail | Slight | Pale buff to cream | 32.5 x 25 | 22–23 | various studies |
| California quail | Moderate | Pale buff to cream | 32 x 25 | 22–23 | various studies |
| Gambel quail | Moderate | Pale buff to white | 31.5 x 24 | 22 | various studies |
| Elegant quail | None | White | 34 x 24 | 22 | this study |
| Bobwhite | None | White | 31 x 25 | 22–23 | Stoddard, 1931 |
| Black-throated bobwhite | None | White to buff | 30.5 x 23 | 24 | this study |
| Spotted wood quail | Slight | Creamy white | 40 x 29 | ? | Wetmore, 1965 |
| Singing quail | None | White & yellow | 31 x 25 | ? | Warner & Harrell, 1957 |
| Harlequin quail | None | White | 32 x 24 | 24–25 | F. Strange, pers. comm. |
| Gray partridge | None | Pale olive | 35 x 27 | 24–25 | McCabe & Hawkins, 1946 |
| Chukar partridge | Moderate | Pale brown or creamy | 45 x 31 | 22–24 | various studies |

Assuming that the fresh egg has an average specific gravity of 1.08 (Barth, 1953), the preceding formula can be modified as follows:

$$\text{Weight (gm)} = .552 \times \text{length (mm)} \times \text{diameter (mm)}^2$$

Using this formula, estimated fresh weights of eggs were calculated from the linear measurements presented in table 7 and are summarized in table 8. In addition, a calculated total estimated clutch weight, based on reported average clutch sizes (see table 12), is indicated as an index to the relative physiological drain on the female in laying an entire clutch. It may be seen that a female's average clutch may represent as little as 20–25 percent of her own weight, as in spruce grouse and ptarmigan, to as much as 90 percent of her weight in certain quail species. Since some of these quail species are persistent renesters, it would seem that such a large investment of energy in a clutch is not detrimental as long as sufficient food is available. Captive bobwhites and other quail regularly lay over one hundred eggs per year (up to three hundred recorded) and may lay as many as five hundred in a lifetime (Kulenkamp and Coleman, 1968), clearly indicating their high capacity for channeling food energy into egg production.

TABLE 8

RELATIONSHIP OF ADULT FEMALE WEIGHT TO ESTIMATED EGG AND CLUTCH WEIGHTS

| | *Est. Egg Weight (gm)* | *Percentage of Female Weight* | *Average Clutch Size* | *Percentage of Female Weight* |
|---|---|---|---|---|
| Sage grouse | 44 | 3.4 | 7.4 | 25.2 |
| Blue grouse | 33 | 3.6 | 6.2 | 22.4 |
| Spruce grouse | 23 | 4.2 | 5.8 | 24.4 |
| Willow ptarmigan | 23 | 3.3 | 7.1 | 23.1 |
| Rock ptarmigan | 21 | 4.1 | 7.0 | 28.7 |
| White-tailed ptarmigan | 21 | 6.4 | 5.2 | 33.3 |
| Ruffed grouse | 19 | 3.8 | 11.5 | 43.7 |
| Greater prairie chicken | 24 | 3.1 | 12.0 | 37.2 |
| Lesser prairie chicken | 24 | 3.3 | 10.7 | 35.3 |
| Sharp-tailed grouse | 24 | 2.9 | 12.1 | 35.1 |
| Mountain quail | 13 | 4.7 | 10.0 | 47.0 |
| Scaled quail | 11 | 6.2 | 12.7 | 78.7 |
| California quail | 11 | 6.7 | 13.7 | 91.8 |
| Gambel quail | 10 | 6.4 | 12.3 | 78.7 |
| Bobwhite | 11 | 6.4 | 14.4 | 92.2 |
| Harlequin quail | 10 | 5.7 | 11.1 | 63.3 |
| Gray partridge | 14 | 3.7 | 16.4 | 60.7 |
| Chukar partridge | 24 | 5.4 | 15.5 | 83.7 |

ing to seemingly different genera. Peterle (1951) reviewed the cases of intergeneric hybrids reported in gallinaceous birds, and Cockrum (1952) provided a more complete survey of hybridization in North American birds. Sibley (1957) commented on the taxonomic significance of hybridization in grouse, and a similar review of the significance of hybridization in the New World quails is available (Johnsgard, 1970). For a complete listing of all known hybrids of gallinaceous birds, including those reported from Europe and Asia, the summary by Gray (1958) may be consulted.

## GROUSE HYBRIDS

Virtually all known cases of hybridization among the North American grouse species have involved naturally occurring hybrids. This is largely a reflection of the difficulties of keeping and breeding grouse in captivity. The only case of hybridization among North American grouse under captive conditions known to me is the production of several hybrids (including reciprocal crosses) between greater and lesser prairie chickens in 1969 and 1970 by William Lemburg of Cairo, Nebraska.* He has also attempted, without success, to obtain backcross hybrids from a wild-caught female greater prairie chicken × sharp-tail grouse mated to males of both of these species.

All of the North American genera of grouse (as recognized here) have been involved in intergeneric hybridization except for *Bonasa* and *Centrocercus*.[1] In addition, intrageneric hybridization has occurred in *Tympanuchus*, *Dendragapus*, and probably also in *Lagopus*.

### *Intrageneric Hybrids*

Hybridization within the genus *Lagopus* has still not been certainly proved, but would seem highly probable on the basis of the extensive area of geographic contact between the willow and rock ptarmigan. Gray (1958) summarized references to British specimens of possible hybrids between these two species but questioned their authenticity. Todd (1963) mentioned one specimen from Labrador that he examined, which he thought might be an abnormally colored willow ptarmigan or possibly a hybrid. Harper (1953) described a subadult male ptarmigan collected in Keewatin that had a bill depth of 8.5 millimeters (vs. 7.75 maximum for his series of rock, and 9–10.5

*William Lemburg, 1970: personal communication.

1. A record of hybridization between the sage grouse and the sharp-tailed grouse has recently been published (*Condor* 73:491–93).

lost after incubation has begun are hard to find. Among the white-tailed ptarmigan Choate (1963) reports one definite renest; and the late clutches number only three or four eggs. Weeden (1965b) reported only one known case of renesting in rock ptarmigan, but noted that 3 percent of 228 nests and broods were late-hatching. Jenkins, Watson, and Miller (1963) mention that among Scottish red grouse definite renesting occurs in some years, and the clutch sizes of second nesting attempts are sometimes smaller than in first ones. They noted that five of seven marked birds laid again after their eggs were taken. Patterson (1949) estimated that a small incidence of renesting probably occurs in sage grouse, and Crunden (1959) subsequently reported one definite case. Stoneberg (1967) found no indication of renesting in the spruce grouse, and so far only two definite cases of renesting in the blue grouse have been reported (Zwickel and Lance, 1965). Renesting by ruffed grouse is apparently infrequent (Bump et al., 1947), with probably less than 25 percent of the unsuccessful females attempting to renest (Edminster, 1947). Ammann (1957) reported that no more than 10 percent of young sharp-tailed grouse hatched in Michigan could have resulted from renesting. Nests of the greater and lesser prairie chickens show a decline in clutch size toward the end of the nesting season (Hamerstrom, 1939; Baker, 1953; Copelin, 1963), suggesting a certain incidence of renesting, but until recently only in the Attwater prairie chicken had any verified cases been reported (Lehmann, 1941). However, Robel et al. (1970) found that three of fourteen radio-tracked greater prairie chicken females renested, one of them making two renesting attempts.

In contrast, the quail as a group show a greater tendency toward double-brooding and renesting, perhaps because of their monogamy and generally more southerly breeding distributions. Leopold (1959) reports that one or two renesting attempts may be made by mountain quail, but very early accounts suggesting that two broods of this species or of scaled quail are sometimes reared are yet to be verified. Evidence favoring double-brooding is strongest for the California and Gambel quails. McMillan (1964) reported that in favorable years up to 75 percent of the early broods of California quail are reared by males while the females renest. McLean (1930) reported one definite second brood in this species. Edminster (1954) states that there may be up to two renesting attempts, and Raitt (1960) stated that a few late broods hatched in August indicate probable renesting behavior. In the Gambel quail renesting attempts are reportedly common until mid-August (Gorsuch, 1934) or even early September (Raitt and Ohmart, 1966), and possible extensive double-brooding during a favorable year has been reported by Gullion (1956a), who believed that the earlier birds may be either cared for by males or left in the care of older birds of the year. Stanford (1953)

## TABLE 12

### Reported Clutch Sizes under Natural Conditions

| *Species* | *Normal Range* | *Mean Clutch Size* | *References* |
|---|---|---|---|
| Sage grouse | 7–13 | 7.39 (154 nests) | Patterson, 1952 |
| Blue grouse | 6–12 | 6.3 (51 nests) | Zwickel & Bendell, 1967 |
| Spruce grouse | 7–10 | 5.8 (39 nests) | Tufts, 1961 |
| Willow ptarmigan | 2–15 | 7.1 (Scotland, 395 nests) | Jenkins, Watson, & Miller, 1963 |
| | | 10.2 (Newfoundland, 106 nests) | Bergerud, 1970b |
| Rock ptarmigan | 3–11 | 7.0 (Alaska, 101 nests) | Weeden, 1965b |
| | | 6.6 (Scotland, 148 nests) | Watson, 1965 |
| White-tailed ptarmigan | 3–9 | 5.2 (11 nests) | Choate, 1963 |
| Ruffed grouse | 6–15 | 11.5 (1473 nests) | Bump et al., 1947 |
| Sharp-tailed grouse | 5–17 | 12.1 (36 nests) | Hamerstrom, 1939 |
| Greater prairie chicken | 5–17 | 12.0 (66 nests) | Hamerstrom, 1939 |
| Lesser prairie chicken | 6–13 | 10.7 (7 nests) | Copelin, 1963 |
| Long-tailed tree quail | 3–6 | . . . . . | Rowley, 1966 |
| Mountain quail | 6–15 | 10.0 (11 nests) | *P. R. Quart.*+ |
| Scaled quail | 5–22 | 12.7 (39 nests) | Schemnitz, 1961 |
| Elegant quail | 8–12 | . . . . . | Leopold, 1959 |
| Gambel quail | 6–19 | 12.3 (40 nests)* | Gorsuch, 1934 |
| California quail | 9–17 | 13.7 (16 nests) | Lewin, 1963 |
| Bobwhite | 7–28 | 14.4 (394 nests) | Stoddard, 1931 |
| Harlequin quail | 6–16 | 11.1 (24 nests) | Leopold & McCabe, 1957 |
| Gray partridge | 9–20 | 16.4 (470 nests) | McCabe & Hawkins, 1946 |
| Chukar partridge | 14–19 | 15.5 (4 nests) | Mackie & Buechner, 1963 |

*Calculated, excluding four obviously incomplete clutches.
+*Pittman-Robertson Quarterly* 8 (1948):10.

## TABLE 15

### Some Reported Population Densities in Favorable Habitats (Expressed in Acres per Bird)

| | | |
|---|---|---|
| Sage grouse: | 51 acres per male on strutting grounds in spring, Wyoming | Patterson, 1952 |
| | 13–21 acres per bird during fall in best habitats, Colorado | Rogers, 1964 |
| Blue grouse: | 9 acres per adult male, summer average, British Columbia | Fowle, 1960 |
| | 2.3–7.7 acres per male on summer range, British Columbia | Bendell & Elliott, 1967 |
| | 2.5 acres per female; 1.3 acres per male, British Columbia | Bendell, 1955a |
| Spruce grouse: | 128 acres per territorial male, Montana | Stoneberg, 1967 |
| | 64–90 acres per male (30% of males territorial), Alaska | Ellison, 1968b |
| Willow ptarmigan (red grouse): | 3.2–12.3 acres per male in spring, Alaska | Weeden, 1965b |
| | 4.5–9.0 acres per pair in spring, Scotland | Jenkins, Watson, & Miller, 1963 |
| Rock ptarmigan: | 56–109 acres per male, spring, Alaska | Weeden, 1965b |
| | 4.9–24.7 acres per territorial pair (peak year), Scotland | Watson, 1965 |
| | 19.8–74 acres per territorial pair (low year), Scotland | Watson, 1965 |
| White-tailed ptarmigan: | 12.8–42 acres per adult in summer, Montana | Choate, 1963 |
| Ruffed grouse: | 8–38 acres per adult during breeding season, New York | Edminster, 1954 |
| | 13.5–30 acres per adult in spring, New York | Bump et al., 1947 |
| | 3.4 acres per adult in spring (based on nests), Michigan | Palmer, 1954 |
| Sharp-tailed grouse: | 45 acres per bird in spring, Michigan | Ammann (in Edminster, 1954) |
| | 16–25.6 acres per bird in late summer, Saskatchewan | Symington & Harper, 1957 |
| Greater prairie chicken: | 10–42.7 acres per bird (summary of 4 studies) | Trippensee, 1948 |
| Lesser prairie chicken: | 17–38 acres per adult male in spring, Oklahoma | Davison, 1940 |
| Mountain quail: | 2 acres per bird maximum spring density, California | Edminster, 1954 |
| Barred & elegant quails: | Under 1 acre per bird locally, Mexico | Leopold, 1959 |
| Scaled quail: | 10.1 acres per bird in winter, Texas | Wallmo, 1956b |
| | 0.84 acres per bird in winter, Oklahoma | Schemnitz, 1961 |

and Copelin (1963) stated that territories of the lesser prairie chicken were only about twelve to fifteen feet in diameter (or 0.002 to 0.004 acres).

Among the quail species, useful application of the principle of territoriality is very limited. Calling or singing by males, at least in the species well studied, denotes the presence of unmated but sexually active males rather than a breeding pair. Thus, in bobwhites, whistling males are simply surplus males (Stoddard, 1931; Bennitt, 1951). The territories of male bobwhites are at most ephemeral and mobile; the female's calls attract sexually active males, whose whistles serve as an advertisement of their presence (Robinson, 1957). The same probably applies to the scaled quail (Schemnitz, 1964). Similarly, in the California quail unmated males establish "crowing territories" near established pairs (Emlen, 1939; Genelly, 1955). Genelly reports that the crowing territories of the excess males may be spaced only about twenty or more feet apart and are as close to established pairs as the latter will allow. Neither California quail nor bobwhites actively defend their nesting sites, and most of the male-to-male fighting involves defense of the mate (Genelly, 1955). In the Gambel quail, pairs gradually form in the winter coveys; the coveys break up as pairs leave and as the unmated males become mutually intolerant and begin to establish individual crowing territories (Raitt and Ohmart, 1966). Estimated winter home range sizes are indicated in table 17 for representative quails. Evidence indicates that the size of these home ranges may vary considerably in different regions and habitats but that they probably average about twenty-five acres in favorable habitats.

The concept of typical territoriality with regard to the gray partridge and the chukar partridge is also of limited application. McCabe and Hawkins (1946) reported that the coveys of gray partridge remain intact until just before nesting. Blank and Ash (1956) report that neither *Perdix* nor *Alectoris* exhibits true territoriality. In the gray partridge establishment of a covey territory is the nearest thing to territorial behavior; covey composition is highly stable in this species. Pairing occurs before the selection of a nesting area, as is also true in New World quails, thus there is no correlation between the selection of mates and the establishment of a nesting area (Blank and Ash, 1956). Mackie and Buechner (1963) agree that typical territoriality is also absent in the chukar partridge. Males repel other males from their mates, thus the female, rather than a geographically defined area, is the object of defense. However, the rally call of mated males may serve to disperse the breeding population in this species (Williams and Stokes, 1965), and population dispersion is thought to be a basic function of avian territoriality.

## TABLE 18

### Some Reported Sex Ratios

### (Expressed as Percentage of Males in Population)

| | Age Class | Percentage Males | Sample Size | References |
|---|---|---|---|---|
| Sage grouse | Immatures | 45.3 | 2,693 | Patterson, 1952* |
| | Adults | 29.6 | 1,964 | Patterson, 1952* |
| | Mixed ages | 40.0 | 7,355 | Rogers, 1964 |
| Blue grouse | Immatures | 50.0 | . . . . | Boag, 1966 |
| | Adults & subadults | 40.0 | . . . . | Boag, 1966 |
| Spruce grouse | Immatures | 48.3 | 766 | Lumsden & Weeden, 1963* |
| | Adults | 55.3 | 423 | Lumsden & Weeden, 1963* |
| Willow ptarmigan (red grouse) | Adults | 55.9 | 2,211 | Jenkins, Watson, & Miller, 1963* |
| Rock ptarmigan | Adults | 58.5 | 1,545 | Watson, 1965* |
| Ruffed grouse | Immatures | 51.2 | 17,577 | Dorney, 1963* |
| | Adults | 54.6 | 5,365 | Dorney, 1963* |
| Sharp-tailed grouse | Immatures | 56.0 | 2,108 | Ammann, 1957 |
| | Adults | 60.0 | 889 | Ammann, 1957 |
| Greater prairie chicken | Immatures | 54.9 | 306 | Baker, 1953 |
| | Adults | 54.6 | 298 | Baker, 1953 |
| Lesser prairie chicken | Immatures | 53.0 | 491 | Lee, 1950 |
| | Adults | 47.0 | 532 | Lee, 1950 |
| Scaled quail | Young adults (1st 18 mo.) | 47.4 | 213 | Campbell & Lee, 1956 |
| | Old adults (over 18 mo.) | 58.9 | 141 | Campbell & Lee, 1956 |
| California quail | Immatures | 50.8 | 6,335 | Francis, 1970* |
| | Adults | 57.3 | 4,347 | Francis, 1970* |
| Gambel quail | Immatures | 49.3 | 333 | Raitt & Ohmart, 1968 |
| | Adults | 57.8 | 154 | Raitt & Ohmart, 1968 |
| | Young adults (1st 18 mo.) | 51.4 | 215 | Campbell & Lee, 1956 |
| | Old adults (over 18 mo.) | 55.8 | 525 | Campbell & Lee, 1956 |
| Bobwhite | Immatures | 50.5 | 34,989 | Bennitt, 1951 |
| | Adults | 59.0 | 7,521 | Bennitt, 1951 |
| Harlequin quail | Mixed (museum sample) | 63.0 | 502 | Leopold & McCabe, 1957 |
| Gray partridge | Adults | 58.0 | 115 | McCabe & Hawkins, 1946 |
| | Mixed | 51.0 | 14,167 | Johnson, 1964* |
| Chukar partridge | Mixed | 50.0 | 116 | Harper, 1958 |

*Calculated from data presented by authors.

## TABLE 19

### Some Reported Fall and Winter Age Ratios
### (Expressed as Percentage of Immatures in Population)

| | *Percentage Immature* | *Sample Size* | *References* |
|---|---|---|---|
| Sage grouse | 57.8% | 4,657 | Patterson, 1952 |
| | 51.4% | 7,355 | Rogers, 1964 |
| Blue grouse | 65% (late summer) | .... | Boag, 1966 |
| | 57–65% | .... | Hoffman et al. (cited in Bendell, 1955a) |
| Spruce grouse | 64.4% | 1,189 | Lumsden & Weeden, 1963* |
| Willow ptarmigan | 72% | 5,266 | Bergerud, 1970b |
| Rock ptarmigan | 73–77% | .... | Cited in Choate, 1963 |
| White-tailed ptarmigan | 33–47% | .... | Choate, 1963 |
| Ruffed grouse | 77% | 22,942 | Dorney, 1963* |
| Sharp-tailed grouse | 70% | 3,926 | Ammann, 1957 |
| | 63.5% | 16,283 | Johnson, 1964* |
| Greater prairie chicken | 50.2% | 604 | Baker, 1953 |
| Lesser prairie chicken | 53.2% | 932 | Lee, 1950 |
| Mountain quail | 48% | 198 | Leopold, 1939† |
| Scaled quail | 74% | 1,219 | Schemnitz, 1961 |
| California quail | 63.3% | 5,603 | Emlen, 1940* |
| | 59.3% | 10,682 | Francis, 1970* |
| Gambel quail | 76% | 352 | Raitt & Ohmart, 1968* |
| Bobwhite | 82.3% | 51,178 | Bennitt, 1951 |
| | 82% | 1,546 | Marsden & Baskett, 1958 |
| Harlequin quail | 61% | 57 | Leopold & McCabe, 1957† |
| Gray partridge | 79.5% | 14,167 | Johnson, 1964* |
| Chukar partridge | 87–89.5% | .... | Johnson, 1960 |

*Calculated from author's data.
†Based on museum skin samples taken at various times of year.

pinnated grouse and the sharp-tailed grouse, the average number of male birds occupying display grounds in general equals or exceeds the number reported for the black grouse. Copelin (1963) indicates that in the display grounds he studied the number of male lesser prairie chickens ranged from 1 to 43, and active grounds averaged 13.7 males over an eleven-year period. Robel's greater prairie chicken study area (1967) had from 17 to 25 resident males present in a three-year period. He found (1966) that 10 marked territorial males defended areas of from 164 to 1,069 square meters (averaging 518 square meters), and that the 2 males defending the largest territories in two years of study accounted for 72.5 percent of fifty-four observed copulations.

Numbers of male sharp-tailed grouse present on display grounds vary considerably with population density in Nebraska; leks of both this species and pinnated grouse average approximately 10 males, but sometimes exceed 20 and occasionally reach 40 or more. Hart, Lee, and Low (1952) reported that up to 100 male sharp-tailed grouse were observed on display grounds in Utah, but the average on twenty-nine grounds was 12.2 males. Evans (1961) confirmed that females select the most dominant males for matings, and Lumsden (1965) reported that on a display ground he studied one male accounted for 76 percent of the seventeen attempted or completed copulations seen. Scott (1950) concluded that the social organization of sharp-tailed grouse is more highly developed than that of the pinnated grouse but is not as complex as that of the sage grouse.

The sage grouse provides the final stage in this evolutionary sequence; it exhibits a higher degree of size dimorphism than any other species of North American grouse (adult weight ratio of females to males being 1:1.6–1.9), the display areas have a larger average number of participating males, and the central territories are among the smallest of any grouse species. Scott (1942) was the first to recognize the hierarchical nature of the territorial distribution pattern and to describe first-rank or master cocks, which were responsible for 74 percent of the 174 copulations that he observed. Dalke et al. (1960) reported that the territories held by master cocks were often forty feet or less in diameter, and Lumsden (1965) showed the territorial distribution of 19 males that exhibited an average distance from the nearest neighbor of about forty feet. In Colorado, 407 counts of strutting grounds indicated an average maximum number of 27.1 males present (Rogers, 1964). Patterson (1952) provided figures indicating that 8,479 males were counted over a three-year period on Wyoming display grounds, averaging about 70 males per display ground. Patterson reported one ground containing 400 males, and Scott's observations (1942) were made on a ground of similar size. Lumsden (1968) found that individual birds may have strutting areas that overlap those of other males, and that

hatched and reared twenty-seven chicks from eggs taken in the wild.

A few records of sage grouse propagation exist, including those of Batterson and Morse (1948) and Pyrah (1963, 1964), who hatched and raised birds from eggs taken in the wild.

Ruffed grouse have probably been raised in captivity more frequently than any other grouse species. Edminster (1947) reviewed the history of this species' propagation in captivity and noted that the first instance of rearing birds from eggs taken in the wild came in 1903 but that A. A. Allen developed the basic techniques needed for successful propagation during the 1920s. Later work by the state game biologists of New York resulted in the rearing of nearly two thousand grouse, including birds of the tenth generation.

Success in rearing and propagating ptarmigans has been quite limited. Seth-Smith (1929b) indicated that willow ptarmigan and the related red grouse were successfully reared in England during the early 1900s, but that the rock ptarmigan had only rarely been kept in captivity. By that time, the pinnated grouse, sharp-tailed grouse, and ruffed grouse had also been maintained in captivity in recent years (Carr, 1969), with rock ptarmigan having been reared from eggs to maturity, and the willow and rock ptarmigans surviving well in captivity after having been caught as adults in the wild. Moss (1969) has described techniques used for hatching and rearing ptarmigan from eggs taken in the wild. He reported success in breeding captive stock over a several-year period, so that breeders four or more generations removed from wild birds have been obtained.

One of the earliest persons to propagate pinnated grouse in captivity was J. J. Audubon, who obtained 60 wild-caught birds in Kentucky. He indicated that many of these birds laid eggs, and a number of young were produced. The history of recent attempts to propagate prairie grouse has been summarized by McEwen, Knapp, and Hilliard (1969), who noted that it is only recently that any real success has been attained with pinnated grouse and sharp-tailed grouse. They have maintained individual greater prairie chickens and sharp-tailed grouse in captivity many years, with one male sharp-tail at least seven years old still vigorous and breeding, and one male pinnated grouse attaining six years of age. From more than forty-four hundred eggs laid by captive birds, 375 pinnated and sharp-tailed grouse were reared by them. Some of the greatest success in rearing prairie grouse in captivity has been by Lemburg (1962). He has been rearing sharp-tailed grouse since 1960 and greater prairie chickens since 1965, and he began raising lesser prairie chickens in 1966. During the last few years he has raised an average of 60 to 70 prairie grouse per year, and in some years has raised as many as 100 birds.

A more meaningful but much more difficult method of evaluating the sporting value of each species is to try to estimate the annual hunter kill for all the states and provinces in which it is legal game. Such estimates are regularly made by most but not all state and provincial game agencies, but since the techniques used for these estimates vary greatly, the accuracy of the estimates varies as well. Nevertheless, in the belief that an inexact estimate is better than none at all, I have attempted to gather annual hunter-kill estimates for all of the species concerned (table 28). In some cases these were derived from annual reports of the game agencies or from technical or semitechnical periodic publications of these agencies, while in others they represent unpublished estimates that are normally used for management purposes or other functions. Because of the diversity of origins of the data, these sources are not indicated in the table, and clearly the estimates should be regarded only as general ones, in spite of the fact that they are not usually rounded off to the nearest thousand. Wherever possible, I have used and averaged figures from a several-year period rather than listed the most recently available single-year's data, since, for grouse in particular, there tend to be major yearly variations in hunter success.

TABLE 28

SOME ESTIMATED RECENT STATE AND PROVINCE HARVESTS, UNITED STATES AND CANADA

| | |
|---|---|
| Alabama: | 2,160,603 bobwhites in 1967. |
| Alaska: | Average harvests from 1952 to 1957 plus 1961, 93,971 ptarmigan, 59,306 total grouse (blue, spruce, ruffed, and sharp-tailed). |
| Arizona: | 6,000 harlequin quail in 1969, average of 40 chukar partridges from 1962 to 1967, and 1,541,978 total other quail (scaled and Gambel) in 1968. |
| Arkansas: | 400,000 bobwhites in 1967. |
| California: | 3,200 sage grouse in 1969, average of 3,471 blue and ruffed grouse, 73,471 chukar partridges, and 2,432,557 quail (mountain, Gambel, and California) from 1963 to 1969. |
| Colorado: | 1968 estimated kill of 13,107 sage grouse, 27,251 blue grouse, 3,382 white-tailed ptarmigan, 2,612 sharp-tailed grouse, 28,127 scaled quail, 4,469 chukar partridges, and 25,249 other quail (Gambel and bobwhite). |

TABLE 28—(continued)

| | |
|---|---|
| Connecticut: | No data on ruffed grouse; a few bobwhites (and released chukars) are killed annually. |
| Delaware: | No data (bobwhite only). |
| Florida: | 2,500,000 bobwhites in 1968. |
| Georgia: | 2,498,587 bobwhites in 1968. The annual ruffed grouse kill is about 2,500. |
| Idaho: | 81,700 sage grouse and 105,600 forest grouse (spruce and ruffed) in 1969. In 1968, 110,000 total quail (mountain, Gambel, California, and bobwhite), and in 1969, 171,200 chukar partridges and 64,700 gray partridges. |
| Illinois: | Average of 2,020,840 bobwhites between 1958 and 1967; average of 9,716 gray partridges from 1961 to 1967. |
| Indiana: | 911 ruffed grouse in 1966; 550,000 bobwhites in 1967; average of 6,960 gray partridges from 1963 to 1964. |
| Iowa: | 720 ruffed grouse in 1968; 750,000 bobwhites in 1967. The annual gray partridge kill averages about 12,000. |
| Kansas: | 46,000 greater prairie chickens in 1967; 3,000,000 scaled quail and bobwhites in 1968. No data on lesser prairie chicken (season closed between 1936 and 1969, 3-day season held in 1970). |
| Kentucky: | Average of 996,000 bobwhites from 1964 to 1967. The annual ruffed grouse kill is usually 30,000–35,000. |
| Louisiana: | 700,000 bobwhites in 1968. |
| Maine: | 273,033 total grouse (ruffed and spruce) in 1968. Ruffed grouse kill from 1955 to 1960 averaged 185,000. |
| Maryland: | No data (bobwhite and ruffed grouse). |
| Massachusetts: | 12,936 bobwhites in 1962. Average yearly kill of ruffed grouse estimated at from 65,000 to 75,000. |
| Michigan: | Average kill of 356,000 ruffed grouse from 1955 to 1960. Sharp-tailed grouse harvest of less than 500 in recent years. No data on bobwhite, which is hunted in only a few counties. |
| Minnesota: | 560,000 ruffed grouse in 1969; 8,833 gray partridges in 1966. No data on spruce grouse. Average sharp-tailed grouse harvest between 1965 and 1969 was 11,000 birds. |
| Mississippi: | 1,250,000 bobwhites in 1967. |

TABLE 28—(continued)

| | |
|---|---|
| Missouri: | 2,810,000 bobwhites in 1967. |
| Montana: | Average harvests between 1964 and 1968 were: sage grouse, 48,964; blue grouse, 53,441; spruce grouse, 33,227; ruffed grouse, 56,408; sharp-tailed grouse, 88,067; chukar partridge, 3,235; gray partridge, 93,717. |
| Nebraska: | 49,000 prairie grouse (pinnated and sharp-tail) in 1969. An estimated total of 15,000 pinnated grouse were taken in 1967. |
| Nevada: | In 1967 the estimated harvest was 7,300 sage grouse, 408 blue grouse, 49,000 chukar partridges (including some gray partridges), and 72,898 total quail (mountain, Gambel, and California). |
| New Hampshire: | No data (ruffed grouse only). |
| New Jersey: | 110,000 ruffed grouse and 111,000 bobwhites in 1969. |
| New Mexico: | Between 1958 and 1968 the average harvest was 1,700 blue grouse, 1,100 pinnated grouse, and 202,000 total quail, including an estimated 162,000 scaled, 36,000 Gambel, and 4,000 bobwhites. |
| New York: | Average harvest of 409,450 ruffed grouse between 1966 and 1969. No data on bobwhites or gray partridges. |
| North Carolina: | 63,043 ruffed grouse in 1964; 2,500,000 bobwhites in 1968. |
| North Dakota: | Sage grouse harvest in 1964 was 100–200 birds. In 1969 the harvest was 5,014 ruffed grouse, 109,255 sharp-tailed grouse, and 69,142 gray partridges. |
| Ohio: | 16,600 bobwhites in 1969; annual ruffed grouse kill estimated to be about 5,000. No recent data on gray partridges, but harvest probably less than in 1959, when 5,400 were taken. |
| Oklahoma: | Average pinnated grouse harvest from 1959 through 1968 was 7,700. In 1968, 3,326,000 scaled quail and bobwhites were harvested, of which an estimated 3,000,000 were bobwhites. |
| Oregon: | 1968 sage grouse harvest was 51,700 and forest grouse (blue, spruce, and ruffed) harvest was 143,300. Blue grouse harvest estimated at 24,476 in 1960. The 1968 total quail |

TABLE 28—(continued)

| | |
|---|---|
| | harvest (mountain, California, and bobwhite) was 216,638, plus 123,000 chukar partridges and 72,500 gray partridges. |
| Pennsylvania: | 1969 harvest was 25,000 bobwhites and 280,000 ruffed grouse. |
| Rhode Island: | Average harvest from 1958 through 1959 was 290 bobwhites and 530 ruffed grouse. |
| South Carolina: | 1968 harvest was 2,500,000 bobwhites. The annual ruffed grouse kill is only 100 to 250 birds. |
| South Dakota: | 1969 harvest was 95,000 prairie grouse and 7,500 gray partridges. In 1967 the pinnated grouse kill was estimated to be 10,000. Sage grouse harvest in 1966 and 1967 about 2,000 birds. Bobwhite harvest 500 in 1959. |
| Tennessee: | 1968 harvest of 1,700,000 bobwhites. The annual ruffed grouse kill is about 15,000 birds. |
| Texas: | 1968 harvest of 8,000,000 bobwhites and 2,000,000 scaled quail. No data on Gambel quail. Average annual lesser prairie chicken harvest from 1965 through 1969 was 275 birds. |
| Utah: | 1967 harvest included 5,089 sage grouse, 17,527 forest grouse (blue and ruffed), 26,187 quail (Gambel and California), 48,906 chukar partridges, and 16,049 gray partridges. |
| Vermont: | No data (ruffed grouse only). |
| Virginia: | 1,380,405 bobwhites in 1968. The annual ruffed grouse kill is about 85,000 birds in good years. |
| Washington: | Average harvests from 1964 through 1969 include 2,483 sage grouse, 162,400 blue grouse, 16,744 spruce grouse, 162,400 ruffed grouse, 113,551 chukar partridges, 25,100 gray partridges, 220,000 California quail, and a few hundred mountain quail, scaled quail, and bobwhites. |
| West Virginia: | 1969 harvest was 66,000 bobwhites and 115,000 ruffed grouse. |
| Wisconsin: | 289,960 ruffed grouse in 1969. Average gray partridge harvest between 1964 and 1968 was 31,835. No data on sharp-tail kill (season closed from 1965 through 1967). |
| Wyoming: | Sage grouse harvest from 1960 through 1969 averaged |

and the outdoors. We are witnessing the progressive extirpation of the greater prairie chicken from one state after another, and we must soon face the possibility that both the Attwater prairie chicken and the lesser prairie chicken will join the heath hen in the shadows of extinction. It also seems unlikely that the magnificent sage grouse will be able to withstand indefinitely the combined onslaughts of sage clearing and sage destruction through herbicide spraying, and it will be fortunate to survive the rest of this century. In Mexico, the fate of the tree quails and the spotted wood quail will become questionable as the cloud forests are progressively ravaged and the previously impregnable and mahogany-rich rain forests of eastern Chiapas are ripped apart by bulldozers, trucks and chain saws. A few short-term advances have been made and are properly rejoiced in, such as the establishment of several grassland refuges for prairie chickens, while at the same time the tide of increasing population and its associated degradation of our natural environment silently inches ever higher and begins to threaten our own survival.

We are not separate from our environment; each species we destroy and each habitat we ravage, whether by bulldozer or pesticides, represents one more bridge that we have burned in our own ultimate battle for survival. It is a melancholy thought that, after its compatriots had disappeared, the last surviving male heath hen in North America faithfully returned each spring to its traditional mating ground on Martha's Vineyard, Massachusetts, where it displayed alone to an unhearing and unseeing world. Finally, in the fall of 1931 it too disappeared. With it died the unique genes that reflected the sum total of the species' history, from Pleistocene times or earlier through uncounted generations of successful survival to the very last, when inbreeding, habitat disruption, fire, and disease inexorably tipped the balance of survival a final time. No one knows exactly how or when that last survivor died, and no bells tolled to mourn its passing. Indeed, only by the absence of its dirge-like booming the following spring was the heath hen's extinction finally established, and the bird that had been as much a part of our New England history as the Pilgrims was irrevocably lost.

# 17

# Pinnated Grouse

*Tympanuchus cupido* (Linnaeus) 1758

OTHER VERNACULAR NAMES

PRAIRIE chicken, prairie cock, prairie grouse, prairie hen.

RANGE

Current resident of remnant prairie areas of Michigan, Wisconsin, and Illinois and from southern Manitoba southward to western Missouri and Oklahoma and portions of the coastal plain of Texas. Also (*pallidicinctus*) from southeastern Colorado and adjacent Kansas south to eastern New Mexico and northwestern Texas.

SUBSPECIES

*T. c. cupido* (Linnaeus): Heath hen or eastern pinnated grouse. Extinct since 1932. Formerly along the East Coast from Massachusetts south to Maryland and north central Tennessee.

*T. c. pinnatus* (Brewster): Greater prairie chicken. Currently limited to several small isolated populations in Michigan, Wisconsin, and Illinois

and to the grasslands of extreme southern Manitoba, northwestern Minnesota, North Dakota, South Dakota, Nebraska, Kansas, and western Missouri.

*T. c. attwateri* Bendire: Attwater prairie chicken. Currently limited to a few isolated populations along the coast of Texas from Arkansas and Refugio counties to Galveston County, and inland to Colorado and Austin counties.

*T. c. pallidicinctus* (Ridgway): Lesser prairie chicken. Currently limited to arid grasslands of southeastern Colorado and southwestern Kansas southward through Oklahoma to extreme eastern New Mexico and northwestern Texas. Recognized by the *A.O.U. Check-list* (1957) as a separate species.

## MEASUREMENTS

Folded wing (greater prairie chicken): males, 217–41 mm (average 226 mm); females, 208–20 mm (average 219 mm).

Folded wing (lesser prairie chicken): males, 207–20 mm (average 212 mm); females, 195–201 mm (average 198 mm).

Tail (greater prairie chicken): males, 90–103 mm (average 96 mm); females, 87–93 mm (average 90 mm).

Tail (lesser prairie chicken): males, 88–95 mm (average 92 mm); females, 81–87 mm (average 84 mm).

## IDENTIFICATION (Greater Prairie Chicken)

Adults, 16–18.8 inches long. Both sexes are nearly identical in plumage. The tail is short, somewhat rounded, and the longer under (but not upper) tail coverts extend to its tip. The neck of both sexes has elongated "pinnae" made up of about ten graduated feathers that may be relatively pointed (in *cupido*) or somewhat truncated (other races) in shape and are much longer in males than in females. Males have a conspicuous yellow comb above the eyes and bare areas of yellowish skin below the pinnae that are exposed and expanded during sexual display. The upperparts are extensively barred with brown, buffy, and blackish, while the underparts are more extensively buffy on the abdomen and whitish under the tail. Transverse barring of the feathers is much more regular in this species than in the sharp-tailed grouse, which has V-shaped darker markings and relatively more white exposed ventrally.

## IDENTIFICATION (Lesser Prairie Chicken)

Adults, 15–16 inches long. In general like the greater prairie chicken, but the darker, blackish bars of the back and rump typical of greater prairie chickens are replaced by brown bars (the black forming narrow margins), the breast feathers are more extensively barred with brown and white, and the flank feathers are barred with brown and dusky instead of only brown. Males have reddish rather than yellowish skin in the area of the gular sacs and during display their yellow combs are more conspicuously enlarged than those of greater prairie chickens. As in that form, females have relatively shorter pinnae and are more extensively barred on the tail.

## FIELD MARKS

The only species easily confused with either the greater or lesser prairie chicken is the sharp-tailed grouse, which often occurs in the same areas where greater prairie chickens are found. Sharp-tailed grouse can readily be recognized by their pointed tails, which except for the central pair of feathers are buffy white, and by their whiter underparts as well as a more "frosty" upper plumage pattern, which results from white spotting that is lacking in the pinnated grouse.

## AGE AND SEX CRITERIA (Greater Prairie Chicken)

*Females* may readily be recognized by their shorter pinnae (females of *pinnatus* average 38 mm, maximum 44 mm, males average 70 mm, minimum 63 mm) and their extensively barred outer (rather than only central) tail feathers. The central crown feathers of females are marked with alternating buffy and darker cross-bars, whereas males have dark crown feathers with only a narrow buffy edging (Henderson et al., 1967). In the Attwater prairie chicken the pinnae of females are about 9/16 inch (14 mm) long, while those of males are over 2 inches (53 mm), according to Lehmann (1941).

*Immatures* may be recognized by the pointed, faded, and frayed condition of the outer two pairs of primaries (see sharp-tailed grouse account). The pinnae length of first-autumn males is not correlated with age (Petrides, 1942).

*Juveniles* may be recognized by the prominent white shaft-streaks, which widen toward the tip, present in such areas as the scapulars and interscapulars.

*Downy young* are illustrated in color plate 61. Downy greater prairie chickens are scarcely separable from those of lesser prairie chickens (see that

account) and also resemble young sharp-tailed grouse. However, prairie chickens have a somewhat more rusty tone on the crown and the upper parts of the body and richer colors throughout. There are usually three (one small and two large) dark spots between the eye and the ear region and several small dark spots on the crown and forehead. Short (1967) mentions, however, that at least some downy specimens of *attwateri* have only one or two tiny postocular black markings, which thus would closely approach the markings of downy sharp-tailed grouse.

## AGE AND SEX CRITERIA (Lesser Prairie Chicken)

*Females* may be identified by their lack of a comb over the eyes and their brown barred undertail coverts, which in males are black with a white "eye" near the tip (Davison, in Ammann, 1957). Males have blackish tails, with only the central feathers mottled or barred, while the tails of females are extensively barred (Copelin, 1963).

*Immatures* can usually be identified by the pointed condition of the two outer pairs of primaries. The outermost primary of young birds is spotted to its tip, while that of adults is spotted only to within an inch or so of the tip. In addition, the upper covert of the outer primary is white in the distal portion of the shaft, whereas in adults the shafts of these feathers are entirely dark (Copelin, 1963).

*Juveniles* are more rufescent than the corresponding stage of the greater prairie chicken or the adults. The tail feathers are bright tawny olive and have terminal tear-shaped pale shaft-streaks (Ridgway and Friedmann, 1946).

*Downy young* (not illustrated) are nearly identical to those of the greater prairie chicken (Short, 1967) but are slightly paler and less brownish on the underparts. On the upperparts the brown spotting is less rufescent and paler, lacking a definite middorsal streak (Sutton, 1968).

## DISTRIBUTION AND HABITAT

The original distribution of the pinnated grouse differs markedly from recent distribution patterns; without doubt it is the grouse species most affected by human activities in North America. Aldrich (1963) identified the habitat of the now extinct eastern race of pinnated grouse, the heath hen, as fire-created "prairies" or blueberry barrens associated with sandy soils from Maryland to New Hampshire or Maine. The presence of oak "barrens" or parklands may have also been an integral part of the heath hen's habitat, particularly in providing acorns as a source of winter foods (Sharpe, 1968).

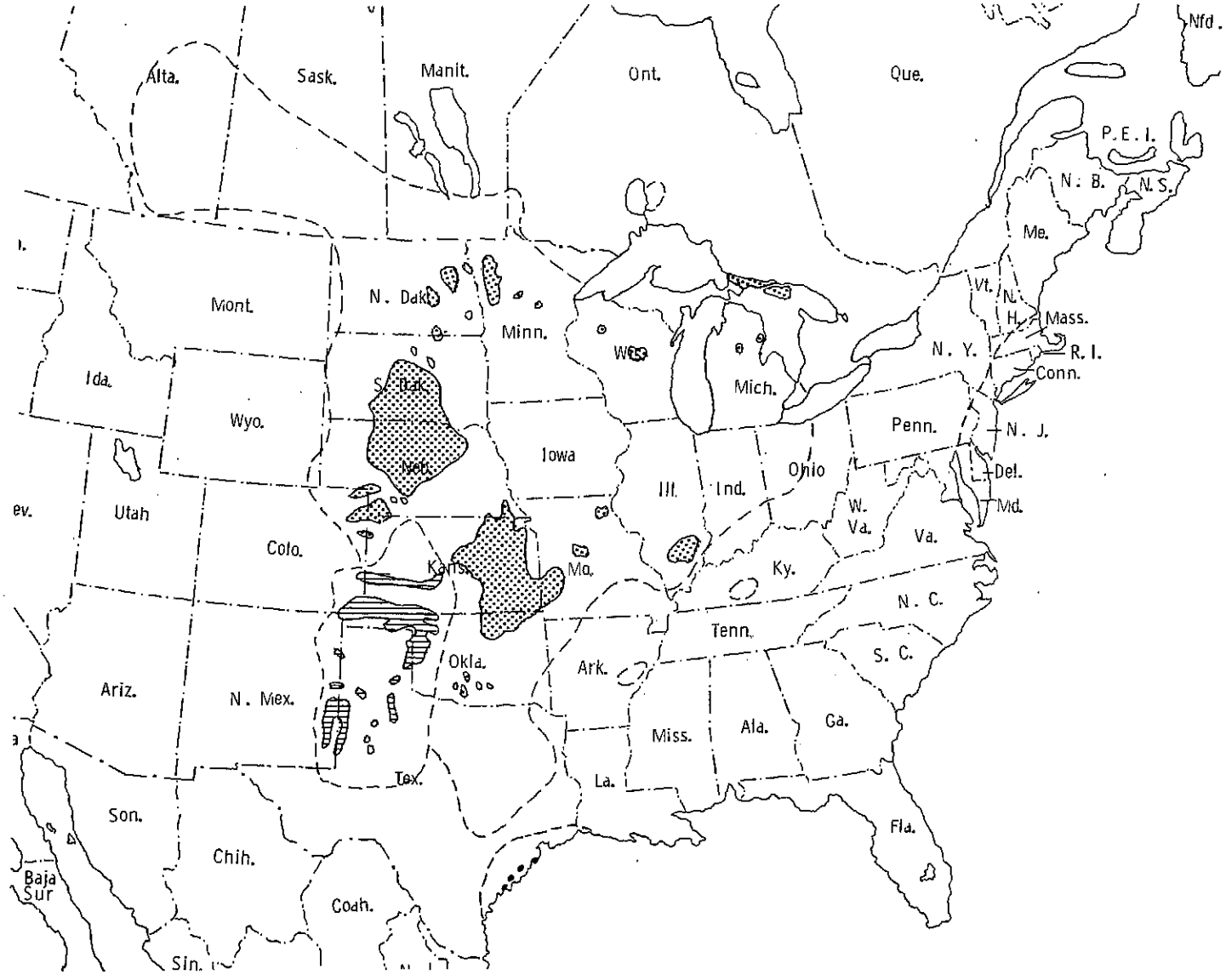


FIGURE 31. Current distribution of the lesser (hatched), greater (shaded), and Attwater (inked) prairie chickens. Original or recent distributions of these forms and the heath hen are indicated by dashed lines.

The range of the coastal Texas race, the Attwater prairie chicken, once extended over much of the Gulf coastal prairie from Rockport, Texas northward as far as Abbeville, Louisiana, an area of more than six million acres (Lehmann and Mauermann, 1963). The lesser prairie chicken once occupied a large area of arid grasslands, with interspersed dwarf oak and shrubs or half-shrub vegetation (Aldrich, 1963; Jones, 1963). The birds occurred over an extensive area from eastern New Mexico and the panhandle of Texas northward across western Oklahoma, southwestern Kansas, and southeastern Colorado. Over this area they were found on two major habitat and soil types, the sand sage—bluestem (*Artemisia filifolia–Andropogan*) shrub grasslands of sandy areas and the similarly sand-associated shin oak–bluestem (*Quercus havardi–Andropogon*) community (Jones, 1963; Sharpe, 1968). The greater prairie chicken originally occurred in the moister and taller climax grasslands of the eastern great plains from approximately the 100th meridian eastward to Kentucky, Ohio, and Tennessee, and northward to Michigan, Wisconsin, Minnesota, and South Dakota (Sharpe, 1968). Sharpe suggested that the presence of oak woodlands or gallery forests throughout much of this range, and the more extensive oak-hickory forests to the east of it may have been an important part of the greater prairie chicken's habitat. Their absence in the western and northwestern grasslands may have made those areas originally unsuitable for prairie chickens. Probably a winter movement of no more than 250 miles to woody cover was typical, according to Sharpe.

With the breaking of the virgin prairies in the central part of North America, and their conversion to small grain cultivation, the prairie chickens responded greatly and moved into regions previously inhabited only by the sharp-tailed grouse (Johnsgard and Wood, 1968). Thus they moved into northern Michigan and southern Ontario, into northern Wisconsin and much of Minnesota, into the three prairie provinces on Manitoba, Saskatchewan, and Alberta, and westward through all or nearly all of North Dakota, South Dakota, and Kansas to the eastern limits of Montana, Wyoming, and Colorado. At the same time the lesser prairie chicken may have undergone a temporary extension northward into western Kansas, northeastern Colorado, and extreme southwestern Nebraska, where it may have been geographically sympatric for a relatively few years with the greater prairie chicken (Sharpe, 1968). However, their habitat requirements are quite different (Jones, 1963), and no natural hybrids between these forms have ever been reported.

During several decades the greater prairie chicken survived extremely well in these interior grasslands, where remaining native vegetation provided the spring and summer habitat requirements and the availability of

cultivated grains allowed for winter survival. Eventually, however, the percentage of land in native grassland cover was reduced to the point that these habitat needs could no longer be provided, and the species began to recede from much of its acquired range and to seriously decline or become eliminated from virtually all of its original range. The sad history of this range restriction and population diminution has been recounted in various places and by many writers (Johnsgard and Wood, 1968). Space does not allow a detailed review of these changes, and all that will be attempted here is a statement of the current range and status of the three extant subspecies.

Of the three races, the Attwater prairie chicken is clearly in the greatest danger of extinction. The race became extirpated from Louisiana in about 1919, and between 1937 and 1963 the Texas population declined from about 8,700 to 1,335 birds (Lehmann and Mauermann, 1963). The remaining population suffers from a badly distorted sex ratio, intensified farming practices, predators, fire exclusion, pesticides, bad drainage practices, and relatively little area set aside specifically for their protection. The purchase of 3,420 acres of land in Colorado County by the World Wildlife Fund in the mid-1960s may be the best hope for the retention of a remnant population. By 1965, when the total Texas population was estimated to be from 750 to 1,000 birds, the estimated refuge population was 100 birds. Lehmann (1968) provided the most recent summary of the status of this bird currently available. As of 1967 an estimated 1,070 birds occupied some 234,000 acres, which represents a habitat loss of 50 percent since 1937 and a population reduction of 85 percent during the same time. No hunting of Attwater prairie chickens is allowed in Texas.

The present range of the lesser prairie chicken centers in the panhandle of northern Texas, but also includes parts of New Mexico, Oklahoma, Kansas, and southeastern Colorado (Copelin, 1963). In Oklahoma the present occupied range consists of 2,391 square miles, and from 1933 to the early 1960s there have been only two years (1950, 1951) when the species could be legally shot (Copelin, 1963). Currently, however, the species is legal game in seven counties, with a nine-day 1970 season. Copelin estimated the 1960 population in Oklahoma to be 15,000 and 30,000 in spring and fall respectively.

In Texas lesser prairie chickens have been almost continuously protected since 1937, but in spite of this protection the populations have declined seriously in recent years as a result of overgrazing, aerial pesticide spraying, and altered farming practices (Jackson and DeArment, 1963). The estimated Texas population in 1963 was no more than 3,000 birds. In 1967, after thirty years of protection, limited hunting of lesser prairie chickens was again established, and seasons were also held in 1968 and 1969. The 1967 Texas

population was approximately 10,000 birds, and the average annual kill through 1969 has been 275 birds. In contrast, the very small Colorado population of lesser prairie chickens may have increased in recent years; Hoffman (1963) reports an increase of from 6 to 104 males on censused display grounds between 1959 and 1962.

In Kansas the distribution and population of the lesser prairie chicken have not been as thoroughly analyzed as in the other states, but Baker (1952, 1953) reported that the drought of the 1930s nearly eliminated the bird from the state. He found that the birds were limited to sandy lands in fourteen counties south of the Arkansas and Cimmaron rivers but did not estimate total population size. The lesser prairie chicken population in these western counties was first protected by a closed season in 1903, which was followed by a period of closed or greatly restricted seasons until the early 1950s (Baker, 1953). In 1970 the lesser prairie chicken was legally hunted over most of its Kansas range on a three-day season. This was the first hunting season that Kansas had established on lesser prairie chickens since 1935. A 1963 population estimate for Kansas was 10,000–15,000 birds (Sands, 1968), and the population has apparently remained at a static level during the last ten years.

The range of the lesser prairie chicken in New Mexico is currently limited to about five counties and centers around Roosevelt County. Except for closed seasons in 1957 and 1959, the species has been legal game every year since that time. The total yearly kill has averaged 1,153 from 1958 through 1968, with a maximum of 2,918 and a minimum of 519 birds. The most recent year for which data are available is 1968, when 776 birds were taken. The New Mexico population is thought to be between 8,000 and 10,000 birds (Sands, 1968).

The total population of the lesser prairie chicken may thus be estimated as a few hundred in Colorado, possibly three thousand in Texas, perhaps fifteen thousand in Oklahoma, ten thousand to fifteen thousand in Kansas, and eight thousand to ten thousand in New Mexico. These estimates would suggest a total population of from thirty-six thousand to forty-three thousand for the bird's entire range.

The status of the greater prairie chicken is almost as alarming as that of the lesser. It now may be regarded as virtually extirpated from all of the Canadian provinces (Hamerstrom and Hamerstrom, 1961). Christisen (1969) has provided a useful summary of the bird's status in the United States. Considering the form's probable original range, it has been extirpated as a breeding species from Iowa, Ohio, Kentucky, Texas, and Arkansas. The birds were gone from Ohio before 1930, and from Kentucky, Texas, and Arkansas at even earlier dates. The last nesting prairie chickens in Iowa

were seen as late as 1952 and stray birds as late as 1960 (Stempel and Rogers, 1961). The estimated population in Indiana diminished from more than four hundred males occupying thirty-three booming grounds in 1942 to four males on a single booming ground by 1966. Christisen (1969) indicates a current estimated total Indiana population of only ten birds.

In Illinois the situation is only slightly better. Although protected since 1932, the population trend has been downward, and an estimated 300 birds remain in the state (Christisen, 1969). The birds are gone from their original ranges in southern Wisconsin and Michigan and persist in small pockets farther to the north, where their total populations are estimated at 1,000 and 200 birds, respectively. In Minnesota the species is also gone from most of its acquired range, and it has been fully protected since 1942, when an estimated 58,300 birds were taken. During its population peak in 1925 an estimated 411,900 birds were killed; by comparison the recent statewide population is estimated at 5,000 (Christisen, 1969).

Virtually all of Missouri might be considered as original greater prairie chicken range (Johnsgard and Wood, 1968), but between the early 1940s and the mid-1960s the species' range diminished from twenty-five hundred square miles to nine hundred square miles, and from nearly fifteen thousand to about seven thousand birds (Christisen, 1967). The birds were last hunted in 1906, and in the last few years the population trend has been upwards, with an estimated ten thousand birds present in the late 1960s (Christisen, 1969).

Colorado, Wyoming, and North Dakota all represent areas of acquired range for the greater prairie chicken. Only eastern Colorado and eastern Wyoming were ever occupied by the birds; June (1967) reports that in Wyoming it is now limited to Goshen County but once occurred also in Laramie County. Its population probably numbers in the hundreds. In Colorado, where it is also protected, the best populations occur in Yuma and Washington counties (Evans and Gilbert, 1969). The most recent state-wide population estimate is 7,600 birds (Christisen, 1969). In North Dakota the birds have been protected since 1945, although prairie chickens are sometimes shot during the sharp-tail season. It arrived in the state in the 1880s, peaked in the early 1900s, and began to decline in the 1930s. Between 1938 and 1942 from 29,000 to 47,000 birds were harvested yearly, and the estimated total population ranged from 300,000 to 450,000 (Johnson, 1964). The present and declining state population is approximately 1,800 birds (Christisen, 1969).

South Dakota's prairie chicken distribution largely represents acquired range, since the species probably originally extended not much farther than the location of the present city of Yankton. No harvest figures are available for the early years of this century, but the populations were probably com-

parable to those of North Dakota during the same era. In both states the drought of the 1930s brought about a severe decline in the number of prairie chickens which probably lasted for much of that decade. Since 1942, prairie chickens and sharp-tails have been hunted every year, with an average combined harvest of about forty thousand birds, sometimes in excess of one hundred thousand. However, prairie chickens are not nearly so abundant as they once were, and they are now largely limited to relatively few counties (Janson, 1953; Henderson, 1964). The highest populations occur in Jones County, where the native grasslands still occupy about 68 percent of the land area and cultivated lands occupy 30 percent; woody cover in South Dakota's prairie chicken range covers less than 1 percent of the total area (Janson, 1953). The 1967 harvest of prairie chickens was about ten thousand birds, and the declining state population is approximately one hundred thousand birds (Christisen, 1969).

In Nebraska the species probably originally occurred in the eastern part of the state, but it is now largely limited to the central portion, where it occurs along the eastern and southern edges of the sandhills, where native grasses and grain crops are in close proximity and provide both summer and winter habitat needs (Johnsgard and Wood, 1968). The state's population is relatively static, and this species as well as the more common sharp-tailed grouse have been regularly hunted, except in the case of the small and isolated population in southeastern Nebraska, which is an extension of the large Flint Hills population of eastern Kansas. In 1967 the estimated Nebraska harvest was fifteen thousand birds, and the state's recent total population was estimated at one hundred thousand birds (Christisen, 1969).

The heart of the greater prairie chicken's present range is in eastern Kansas, amid the bluestem (*Andropogon*) prairies that extend from the Oklahoma border in Chautauqua and Cowley counties to near the Nebraska border in Marshall County (Baker, 1953). This zone includes an easternmost zone of interspersed natural grassland and croplands, a zone of sandy soils associated with natural grasslands and wooded hilltops, a zone of flinty, calcareous hills and associated native grasslands, and a transition zone between these hills and the cultivated lands to the west. In the best areas for prairie chickens, the ratio of natural grasslands to cultivated feed crops is roughly two to one (Baker, 1953). Prairie chickens have been given protection in Kansas periodically since 1903. The population apparently underwent a marked decline in the early 1940s, followed by an increase to the end of that decade, when fifty thousand birds were conservatively estimated to be present in the state (Baker, 1953). In 1967 some forty-six thousand birds were harvested, and an estimated seven hundred and fifty thousand were believed present in the late 1960s (Christisen, 1969), suggesting that the Kansas pop-

ulation is by far the most secure of any state's.

The only remaining state still supporting greater prairie chickens is Oklahoma. They probably once inhabited all of eastern Oklahoma, but they are now largely restricted to the northeastern corner of the state north of the Arkansas River. Besides occurring in eight of these northeastern counties, birds have apparently been successfully restocked in four more southerly and westerly counties (Sutton, 1967). In contrast to all other states, the population trend in Oklahoma for prairie chickens is upward (Christisen, 1969), and in both 1967 and 1968 between thirteen thousand and fourteen thousand were killed. In contrast, the 1959 to 1968 average yearly kill was under eight thousand birds. Although Oklahoma has not invested in prairie chicken refuges, its successful restocking program combined with a policy of converting marginal timberlands and agricultural lands to natural grasslands has evidently been the major reason for the recent improvement in greater prairie chicken populations.

In summary, it would seem that the total collective populations for the three extant prairie chicken forms might be one thousand for the Attwater, fifty thousand for the lesser, and perhaps up to a million greater prairie chickens, with three-fourths of the last-named confined to the state of Kansas. Only in Kansas, Oklahoma, Nebraska, and South Dakota can the greater prairie chicken populations be considered safe, and in South Dakota the population is declining. Paradoxically, in none of these states is land being set aside by public agencies for prairie chicken populations, although this has been done for marginal populations in Indiana, Michigan, Illinois, Wisconsin, Missouri, and North Dakota (Christisen, 1969).

## POPULATION DENSITY

Population density estimates for prairie chickens vary greatly for different areas and in general probably reflect the deteriorating status of the species, with declining populations being studied more intensively than the relatively few healthy or increasing populations. Grange (1948) estimated a spring prairie chicken population in Wisconsin of 1 prairie chicken per 110 acres in 1941 and 1 per 138 acres in 1942, or between 4 and 6 birds per square mile. In 1943, the prairie chicken range in Missouri likewise averaged 4.8 birds per square mile. In South Dakota's best remaining prairie chicken habitat of six counties, spring population densities of from 2 to 4 birds per square mile occur (Janson, 1953).

In contrast, Baker (1953) studied several flocks of prairie chickens in high-quality Kansas range on a study area covering about 3½ square miles. Two flocks used this area exclusively, while two other flocks used it in part.

Spring numbers of one flock varied over a three-year period from 15 to 104 birds, while a second flock varied from 15 to 43 birds during these three springs. A third flock consisted of about 20 birds. Using conservative figures, an average spring population of at least 50 birds must have been dependent on the area, or at least 14 birds per square mile. During population "highs," the spring density may have reached about 50 birds per square mile for the study area as a whole, and even more if only the composite home range areas are considered.

Data on male spring densities for the lesser prairie chicken are available from Oklahoma (Copelin, 1963). Over a six-year period on four different study areas having display grounds, the densities of males per square mile varied from 1.5 to 18.31 and averaged 7.4 males. Earlier figures available from one of these study areas for the 1930s indicated densities of from about 15 to nearly 40 males per square mile. Hoffman (1963) reported that male densities on three areas in Colorado increased from 0.8 to 5.8 males per square mile over a four-year period in this marginal part of the species' range. In Texas, Jackson and DeArment (1963) noted that numbers of males on a 100,000 acre area reached as high as 600 birds in 1942 (about 4 birds per square mile) but more recently have averaged about 200 males. These data would collectively indicate that spring densities of males in favorable habitats may exceed 30 per square mile, but probably average less than 10. Similarly, Lehmann (1941) reported spring densities of about 10 birds per square mile for the Attwater prairie chicken in Texas for the late 1930s. A 1967 survey of this population indicated that 645 birds were present on about 136,000 acres, or a density of 210 acres per bird (3 birds per square mile).

## HABITAT REQUIREMENTS

### *Wintering Requirements*

The winter requirements for pinnated grouse seem to center on the availability of a staple source of winter food, rather than protective cover or shelter from the elements. Lehmann (1941) reports for the Attwater prairie chicken that the birds moved into lightly grazed natural grassland pastures by mid-November and remained there until spring. In Oklahoma, Copelin (1963) found that the lesser prairie chickens used cultivated grains, especially sorghum, extensively during two winters. In the following winter, when production in the shin oak grassland pastures was apparently high, the birds remained in this pastureland area. During the following two winters increased usage of cultivated grains occurred, particularly in late winter when snow was nearly a foot deep for a week or longer, and shocked grain sorghum was then extensively utilized.

Edminster (1954) concluded that grainfields represent an important part of present-day prairie chicken habitat, with corn providing the best winter habitat, provided that it is either shocked or left uncut. Sorghum, like corn, stands above snow during the winter and thus is almost as valuable. Robel et al. (1970) confirmed the importance of sorghum in winter for Kansas prairie chickens. Other small grains such as wheat and rye are utilized whenever they can be reached by the birds during winter.

In contrast to the sharp-tailed grouse and nonprairie grouse, there is little evidence that the pinnated grouse ever resorts to buds as a primary source of food during winter. Martin, Zim, and Nelson (1951) list the buds and flowers of birch as a minor source of winter food for pinnated grouse from the northern prairies but found them of far less importance than cultivated grains or wild rose (presumably rose hips). Edminster (1954) lists the buds of birches, aspens, elm, and hazelnut among items used in the northern range during winter, but so long as grain or other seed sources are available this would not appear to be critical to winter survival. Mohler (1963) reported that the best winter habitats for prairie chickens in the Nebraska sandhills were areas where cornfields were located near the extensive and lightly grazed grasslands of the larger cattle ranches, providing a combination of available food and grassy roosting cover.

*Spring Habitat Requirements*

The habitat requirements of the lesser prairie chicken for display ground locations have been summarized by Copelin (1963). He reported that the males always selected areas with fairly short grass for display grounds and that the grounds were usually located on ridges or other elevations. In sand sagebrush habitat, display grounds on the other hand were located in valleys on short-grass meadows if the sagebrush on adjacent ridges was tall and dense. Lehmann (1941) noted that of several hundred Attwater prairie chicken booming grounds studied, most were on level ground or slightly below the adjacent land surface, but they typically consisted of a short-grass flat, about an acre in extent, surrounded by heavier grassy cover.

Ammann (1957) has provided similar observations for the greater prairie chicken in Michigan. He noted that of sixty-five prairie chicken and ninety-five sharp-tail display grounds observed, 47 percent were located on elevated sites and only four were in depressions. Of ninety-seven Michigan prairie chicken grounds studied in 1941, twenty-seven contained some woody growth other than sweet fern or leather leaf, while of sixty-five grounds studied since 1950 only two contained a sparse stocking of woody

cover. Prairie chickens evidently will not tolerate as much woody cover on their booming grounds as will sharp-tailed grouse.

Robel et al. (1970) found that booming grounds in Kansas were associated with clay pan soil types, and the birds remained on these sites for some time after display activities ceased, feeding on succulent green vegetation, especially forbs. With the coming of hot summer weather, the steep limestone hillsides received greater use, probably because of the availability of shade for loafing. Lehmann (1941) likewise reported that heavy shrub cover provides shade for hot summer days, protection against predators and severe weather, and a source of fall food.

In a comparison of habitat requirements of greater and lesser prairie chickens, Jones (1963) found that both forms preferred level or elevated sites associated with short grasses. Plant cover differences were not significant, but greater prairie chickens tolerated somewhat taller vegetation than did the lesser (a mean of 15.1 cm versus 10.4 cm). Anderson (1969) reported that greater prairie chickens preferred grass cover less than six inches tall for their booming grounds, the combination of short cover and wide horizons apparently being far more important than the specific cover type present on the land.

*Nesting and Brooding Requirements*

Ammann (1957) indicated that of thirteen prairie chicken nests found in Michigan, eight were in hayfields, one was in sweet clover, three were in wild land openings, and one was located on an airport. All of the nests were in fairly open situations. Hamerstrom (1939) has similarly reported on twenty-three prairie chicken nests in Wisconsin. Eleven of these were in grass meadows near drainage ditches, three were in dry marshes or marsh edges, three were in openings or edges of jack pine–scrub oak woods, three were in scattered mixtures of brush, small trees, and grass, two were in small openings in light stands of brushy aspen or willow, and one was in rather dense mixed hardwoods. Both of these studies indicate the importance of grassy, open habitats for prairie chicken nests. Hamerstrom, Mattson, and Hamerstrom (1957) and Yeatter (1963) have both emphasized the importance of mixed natural grasslands or substitutes in the form of redtop (*Agrostis alba*) plantings as nesting and rearing cover types for prairie chickens. Yeatter (1963) correlated a decline in redtop production and prairie chicken populations in Illinois and found that birds nesting in redtop had a nesting success as high as or higher than those using pastures, idle fields, or waste grasslands.

Schwartz (1945) also provided information on nest site preferences in

greater prairie chickens, and noted that of fifty-seven nest locations, 56 percent were in ungrazed meadows. Half the remainder were in lightly grazed pastures, while the others were in sweet clover, fencerows, sumac, old cornfields, or barnyard grass. The usual proximity of nests to booming grounds has led Schwartz, Hamerstrom (1939), and Jones (1963) to comment on this relationship. However, Robel et al. (1970) found considerable movements between booming grounds by females and questioned that the location of booming ground has any major influence on female nesting behavior. He found that nineteen nest sites averaged 0.68 miles from display grounds, and ranged up to 1.13 miles away. Jones (1963) noted that all of the nine greater prairie chicken nests he found were located near pastures or old fields that had a large number of forbs into which the broods were taken following hatching.

Lehmann (1941) reported that of nineteen Attwater prairie chicken nests found, seventeen were in long-grass prairie, one was in a hay meadow, and one was in a fallow field. All of them were located in the previous year's grass growth, and fifteen were in well-drained situations, often on or near mounds or ridges. Twelve were located near well-marked trails, such as those made by cattle. All of the nests were roofed over with grassy vegetation, and most had good to excellent concealment characteristics. Copelin (1963) reported on nine lesser prairie chicken nests in Oklahoma and Kansas. None of these occurred among shrubs more than fifteen inches high, and seven were located between grass clumps, particularly little bluestem (*Andropogon scoparius*). Two were under bunches of sage, and one was under tumbleweed. Shin oak shrubs from twelve to fifteen inches tall were associated with five of the nests.

Following hatching, females with broods typically moved to somewhat heavier cover than was utilized for nesting. Copelin (1963) noted that only one brood of lesser prairie chickens was found in the low shinneries of oak, but twenty-seven were seen in oak motts, which are clumps of oak four to twenty feet tall in stands up to one hundred feet in diameter. Oak motts provide better shade than do oak shinneries. In the absence of oak, the birds moved into cover provided by sagebrush or other bushy plants. Lehmann (1941) likewise found a movement of both young and old Attwater prairie chickens toward cover that provided a combination of shade and water. The importance of free water for prairie grouse is questionable (Ammann, 1957), but certainly in moister habitats the availability of succulent plants, insects, and shade all contribute to the value of the area as rearing cover.

Yeatter's (1943, 1963) studies in Illinois indicated that females with newly hatched young feed mainly in redtop fields and to some extent in small grain or grassy fallow fields. They also move along ditch banks and field

borders, where there is heavier cover. In Missouri, females take their young to swales that provide cover in the form of slough grass, where a combination of shade, protection, and easy movement is present. As the birds grow older, they gradually move to higher feeding grounds such as grainfields or stubble but still return in the heat of the day to rest in the shade provided by shrubs, large herbs, or trees.

## FOOD AND FORAGING BEHAVIOR

Winter foods of the prairie chicken are virtually all from plant sources (Judd, 1905b; Schwartz, 1945). Judd indicated that the prairie chicken consumes only about half as much mast as does the ruffed grouse, consisting mostly of the buds of poplar, elm, pine, apple, and birches. It also consumes some hazelnuts (*Corylus*) and acorns, which it swallows whole. In most parts of the bird's present range, however, grain is much more important than buds as winter food. As noted earlier, corn and sorghum represent major winter foods for the species, with corn more important in northern areas and sorghum of increasing importance farther south.

Korschgen (1962) found that in Missouri corn kernels and sorghum seeds are the primary winter foods, with corn remaining important well into spring. In late spring, soybeans (*Glycine*) exceed corn in usage, with the leaves being consumed first and later the seeds and seed pods. Sedge (*Carex*) flower heads are also important in the spring diet, as are grass leaves. Two cultivated grasses, oats and wheat, are heavily depended on in summer, first for their leaves and later for their grains. Korean lespedeza (*Lespedeza*) foliage is used almost throughout the year, but especially from July through September. In September ragweed (*Ambrosia*) seeds begin to appear in the diet and are used to a limited extent until February.

On a year-round basis, Judd (1905b) reported that animal foods (mostly grasshoppers) constitute about 14 percent and plant foods 86 percent of the greater prairie chicken's diet. Martin, Zim, and Nelson (1951) stated that during summer the animal portion may reach 30 percent but in winter and spring is as little as 1 to 3 percent. Lehmann (1941) found that adults of the Attwater prairie chicken consume about 88 percent plant material and 12 percent insect food, with seeds and seed pods alone comprising more than 50 percent of the materials eaten. In contrast to the high percentage of cultivated grains found in most studies of the greater prairie chicken, native plants found in lightly grazed pastures provided the major food items listed by Lehmann. These included ruellia (*Ruellia*), stargrass (*Hypoxis*), bedstraw (*Galium*), doveweed (*Croton*), and perennial ragweed

(*Ambrosia*) as well as many other less important species.

Jones's study (1963) of the greater and lesser prairie chickens in Oklahoma brought out some striking differences in foods taken in study areas about two hundred fifty miles apart. The percentage of insects consumed was much higher in the case of the lesser prairie chicken (41.8 and 48.6 percent average yearly volume in two habitats) than was true of the greater prairie chicken (8.2 and 20.8 percent average volume in two habitats). The remainder of the food of both species consisted of seeds and green vegetation, with the latter usually comprising more volume than the former. Both species fed in grassy cover, but whereas lesser prairie chickens preferred mid-length grasses for foraging, the greater was found feeding more frequently in short grasses. Jones also reported (1964b) that during the six-month period when plants were important food items, the half-shrub cover type (associated with sandy soils) was used for foraging for five months, and the short-grass cover type (associated with clay soils and used for display purposes) was heavily used only during April. Copelin (1963) reported that the relative use of sorghum in winter was closely related to the amount of snow cover, with large flocks moving to grainfields when snow was about a foot deep for a week or more. When such snow is present, lesser prairie chickens regularly make snow roosts (Jones, 1963), suggesting a fairly recent climatic adaptation to the warmer climates typical of the bird's present range.

## MOBILITY AND MOVEMENTS

An early analysis of greater prairie chicken seasonal movements was made by Hamerstrom and Hamerstrom (1949) for the Wisconsin population. They suspected that little movement occurred during summer, especially during the brood-rearing period. However, during autumn considerable movement does occur, and some slight migratory movements may exist. Autumn movements of up to twenty-nine miles were established using banded birds, which perhaps correspond to the "fall shuffle" of quail or the general fall dispersion of young birds known for other grouse. Most of the longer movements found were those of females; six of the eight females recovered had moved at least three miles, while eighteen of thirty males had moved less than three miles.

During winter, prairie chickens typically occur in large packs formed by mergers of the fall packs. In Wisconsin these consist of up to one hundred to two hundred birds, which become progressively less mobile in the most severe weather. During very bad weather the birds move very little and may

scarcely leave their winter roosts. Roosting sites in the Hamerstroms's study area were often from a quarter to a half mile from feeding fields and were seldom more than a mile and a quarter away.

By February, the winter packs begin to break up and the males start returning to their booming grounds. The Hamerstroms found that fifty-six banded males usually moved less than two miles from their winter feeding grounds to their booming grounds (fifty of fifty-six birds), while the remaining six males moved from two to eight miles. Apparently many males winter at feeding sites which are the nearest available ones to their booming grounds, and in late winter some daily movements between these locations may occur. During spring there is little movement on the part of males; the birds may roost on their territories or within a few hundred yards of it. Sources of water, shade, dusting places, and loafing sites are often within a half mile. Following the termination of display activities, the males may remain close to their booming grounds for much of the summer.

More recent studies of movements of greater prairie chickens have been made by Robel et al. (1970) in Kansas, using radio telemetry. They established monthly ranges for thirty-nine adult males, thirty-seven adult females, and thirty-one juveniles. Movements of adult males were greatest in February, as the birds began to visit their booming grounds and also had to search somewhat harder for food. Flights of a mile or more between feeding areas and display grounds were sometimes seen, and there was also some movement between display grounds. Immature males, however, exhibited their greatest movements in late February and March, with the later flights undertaken largely between display grounds as the birds unsuccessfully attempted to establish territories at various grounds. During April and May both adults and immatures exhibited reduced movements, with the birds remaining closely associated with specific booming grounds. Maximum movements of females occurred in April, during the time of peak male display. Females often visited several different booming grounds, with movements of up to 4.8 miles being recorded. One female that attempted to nest three times was fertilized at a different booming ground prior to each nesting attempt. Summer movements by both sexes were minimal, as the birds molted and females were rearing broods. However, during fall, longer movements again became typical, especially among juveniles. Three juvenile males moved distances of from 2.7 to 6.7 miles during October and November, but comparable data for females are not available. However, daily movements of females during that time averaged farther than those of males (808 yards versus 660 yards).

Monthly movements of the prairie chickens studied by Robel et al. (1970) reflect this seasonal behavior pattern. Summer monthly ranges of

adult males were greatest in June (262 acres), fairly small in July (132 acres), and smallest in August (79 acres). In fall and winter the monthly ranges increased from 700 to almost 900 acres from November to February and reached 1,267 acres in March then decreased sharply and were at a minimum of 91 acres in May. Data for juvenile males indicated a similar monthly mobility pattern for the year. On a daily basis, adult males were most highly mobile in February (with an average daily movement of 1,121 yards), and they decreased their daily mobility through August (320 yards per day). The movements increased again in fall and through the winter averaged from 600 to 700 yards per day until February. During the period of February through September, adult females had average daily movements of from 332 to 928 yards. Juveniles of both sexes had daily movements rather similar to those of adult males, being least extensive in August and increasing to a peak in March.

Comparable data for the lesser prairie chicken are not available, but Copelin (1963) does provide some observations on mobility. He also found that movements were most limited in summer and most extensive in winter. The summer range of a female and her brood was estimated to be from 160 to 256 acres, or somewhat less than the estimates of monthly summer mobility in greater prairie chicken females. On the basis of observations of 114 banded birds, 79 percent were found within 2 miles of their point of capture, and 97.4 percent were within 4 miles. The maximum known distance of movement was 10 miles. In common with the Hamerstroms's study, he found that juveniles often moved considerable distances between their brood ranges and display grounds the following spring, with all of fourteen birds moving at least 0.5 mile, and two moving nearly 3 miles. Considering birds captured in fall and winter and observed the following spring on display grounds, he found that juvenile birds tended to move farther than adults during this time and that juvenile hens moved farther than juvenile males. Forty juvenile males moved an average distance of 0.93 miles and twenty adult males moved an average of 0.46 miles. Six juvenile hens moved an average distance of 2.12 miles and one adult hen moved 3.75 miles.

Lehmann (1941) provided some observations on seasonal movements in the Attwater prairie chicken which in general support the studies already discussed. He noted a summer movement of adult and fairly well grown young from nesting areas into heavier summer cover that provided shade and water, followed by a sedentary state until fall. At this time, from September onward, the birds moved out of some pasturelands and into others that provided winter food and cover conditions. During this time, large concentrations of up to 250 to 300 individuals were sometimes seen,

in addition to many smaller flocks of 8 birds or fewer. These winter packs break up late in January, when males begin to display.

## REPRODUCTIVE BEHAVIOR

### *Territorial Establishment*

As in the sharp-tailed grouse, fall establishment of territories and associated fall display occurs regularly in the pinnated grouse. Copelin (1963) noted that during the fall old male lesser prairie chickens reestablish territories that they held during the spring, and although young males visit the booming grounds, they are apparently not territorial. In the greater prairie chicken an active period of fall display is likewise a regular phenomenon, at least in Missouri (Schwartz, 1945), Michigan (Ammann, 1957), and various other states, although Hamerstrom and Hamerstrom (1949) did not regard it as typical in Wisconsin. Whether or not the females regularly visit the grounds during fall is not so important as the fact that territorial boundaries are reestablished by mature and experienced males, and young males learn the locations of these display grounds. During the following spring some shifting about may occur as deaths among the males during the winter remove some territory holders, but the basic structure of the booming ground is probably formed during fall display.

The average size of the lek, in terms of participating males, is similar to that of sharp-tailed grouse. Lehmann (1941) indicated that for five Attwater prairie chicken grounds studied over a three-year period, the average yearly numbers of participating males ranged from 7.2 to 8.4. Grange (1948) indicated that on seventeen display grounds in Wisconsin in 1942, an average of 6.9 males were present. In Nebraska, an average of about 9 male prairie chickens is typical of booming grounds (Johnsgard and Wood, 1968). Generally similar figures have been indicated for Missouri (Schwartz, 1945) and Illinois (Yeatter, 1943). The largest reported booming grounds were those noted by Baker (1953) for Kansas; he observed one ground containing approximately 100 males.

Copelin (1963) summarized numbers of male lesser prairie chickens on display grounds in Oklahoma from 1932 to 1951. For a total of 64 grounds studied over varying periods of years, the average number of males present was 13.7 and was as high as 43. These grounds occurred on a study area of sixteen square miles, and in different years from as few as 8 to as many as 40 display grounds were found on this study area. The average figure of 24 display grounds would indicate that good lesser prairie chicken habitat might support about 1.5 active display grounds per square mile. Baker

(1953) indicated that 6 greater prairie chicken booming grounds were present on a study area of about 3.5 square miles of excellent range in Kansas, or 1.7 grounds per square mile. Most other studies indicate a greater scattering of display grounds for the greater prairie chicken, which may be in part a reflection of the effective acoustical distances associated with the male vocal displays. The lower-pitched booming calls of the greater prairie chicken presumably are effective over greater distances than are the homologous "gobbling" calls of the lesser prairie chicken, and this might affect spacing characteristics of display grounds.

*Male Display Behavior*

Since the basic sexual and agonistic behavioral patterns of the greater, lesser, and Attwater prairie chickens are virtually alike, a single description of motor patterns will be given, with comments on any differences that might occur, based on Sharpe's comparative analysis of the three forms (1968).

Booming is the collective term given to the sequence of vocalizations and posturing of greater prairie chicken males that serve both to announce territorial residence to other males and to attract females. During booming, the tail is elevated, the pinnae are variably raised to a point that may be almost parallel with the ground, the wings are lowered while held close to the body, and the primaries are spread somewhat. The bird then begins a series of foot-stamping movements (about twenty per second according to Hjorth, 1970), during which he moves forward a relatively short distance, followed by a multiple snapping of the tail in three rapid fanning movements. At the same time as the tail is initially clicked open and shut, a three-syllable vocalization ("tooting" of Hjorth, 1970) begins, lasting almost two seconds and sounding like *whoom-ah-oom*, with the middle note of reduced amplitude. During the second note a rapid and partial tail-fanning also occurs and the "air sacs" are partially deflated. During the third note the esophageal tube is again inflated and the lateral apteria or "air sacs" are maximally exposed. Simultaneously, the tail is rather slowly fanned open and again closed. Sharpe (1968) indicated that in the lesser prairie chicken a single, exaggerated tail-spreading movement occurs during the first phase of booming and the latter tail-spreading elements are lacking. He estimated that the maximum amplitude of the fundamental harmonic during booming is about 300 cycles per second (Hz) in the greater and Attwater prairie chicken and about 750 Hz in the lesser prairie chicken. In addition, the vocalization phase of the lesser lasts about 0.6 seconds, as opposed to nearly 2 seconds in the greater. The associated call ("yodelling"

of Hjorth, 1970) sounds more like a "gobble" and has two definite syllables plus a terminal humming sound. However, "low-intensity" booming may have up to four syllables. Hjorth (1970) has distinguished a variant of the lesser prairie chicken's gobbling call which he called "bubbling," but it appears to be an incomplete and less stereotyped version of the more typical call and posture and probably corresponds to Sharpe's "low intensity booming." In contrast to the greater prairie chicken, male lesser prairie chickens frequently utter their booming displays in an antiphonal fashion ("duetting" of Hjorth, 1970), with up to ten displays being performed in fairly rapid sequence. An additional visual difference between the displays of the two forms is that the exposed gular sac of the lesser is mostly red, whereas those of the greater and Attwater prairie chickens are yellow to orange (Jones, 1964a; Lehmann, 1941).

A second major display of prairie chickens is flutter-jumping. It is performed in the same fashion by this group as by sharp-tailed grouse and no doubt serves a similar advertisement function. Unlike that of the sharp-tail, however, most prairie chicken flutter jumps have associated cackling calls ("jump-cackle" of Hjorth, 1970). Sharpe (1968) found that calls occurred during twenty-seven of thirty flutter jumps in Attwater prairie chickens, sixteen of twenty in lesser prairie chickens, and seventeen of twenty in greater prairie chickens. He noted that flutter-jumping is especially typical of peripheral males when hens are present near the middle of the display ground.

When defending territories against other males, several display postures and calls are typically seen. Ritualized and actual fighting, such as Lumsden (1965) described for the sharp-tailed grouse, is commonly seen, often with short jumps into the air and striking with the feet, beak, and wings. Between active fights, the males will commonly "face off," lying prone a foot or two apart and calling aggressively. Associated calls during facing off include a whining call much like that of sharp-tails, and similar more nasal "quarreling" note (Sharpe, 1968) that sounds like *nyah-ah-ah-ah*. Grange (1948) describes the "fight call" as a very loud, raucous *hoo'-wuk*. Apparent displacement sleeping, displacement feeding, and "running parallel" displays have also been noted by Sharpe at territorial boundaries. A white shoulder spot is often evident in such situations and Hjorth (1970) noted that in both sexes of lesser prairie chickens this may frequently be observed.

When a female enters a male's territory, his behavior changes greatly. Booming is performed with high frequency and extreme posturing, particularly as to pinnae erection and eye-comb enlargement. The eye-combs of all three forms are a bright yellow, but those of the lesser prairie chicken are relatively larger than those of either the greater or Attwater prairie chicken.

Between booming displays, the male will sometimes stop and "pose" before the female while facing her, but most booming displays are not oriented specifically toward the hen. Rather, the male circles about her and all aspects of his plumage are visible to her.

In the presence of females, when they are either nearby or at some distance, a characteristic *pwoik* call ("whoop" of Hjorth, 1970) is frequently uttered (Lehmann, 1941). Sharpe reports that this call is very similar in both the greater and Attwater prairie chickens, but in the lesser it is higher pitched and sounds like *pike* ("squeak" of Hjorth, 1970). It lasts for a shorter duration (0.23 seconds compared to about 0.4 seconds in the larger forms) and the greatest sound amplitude occurs at about 1,000 Hz, rather than 550 to 600 Hz.

All three forms of prairie chickens perform the "nuptial bow" ("prostrate" of Hjorth, 1970), which Hamerstrom and Hamerstrom (1960) originally described for the greater prairie chicken. They regarded it as a sexual display that often precedes copulation and yet is not a prerequisite for it. Sharpe (1968) found that the same applies to the Attwater and lesser prairie chickens, and in all three the display has the same form. The male, while actively booming and circling about a nearby female, suddenly stops, spreads his wings, and lowers his bill almost to the ground while keeping his pinnae in an erect posture. He may remain in this posture for several seconds as he faces the female.

When females are ready for copulation they squat in the typical galliform manner, with wings slightly spread, head raised, and neck outstretched. When mounting, males grasp the female's nape, lower their wings on both sides of her, and quickly complete copulation. After copulation, females usually quickly run forward a few feet then stop to shake. Males lack any specific postcopulatory displays and often begin booming again within a few seconds.

### *Vocal Signals*

In addition to the booming, whining, quarreling, and *pwoik* calls already mentioned, pinnated grouse have several other vocal signals. Many cackling sounds are also uttered. Sharpe (1968) recognized a "long cackle" that consists of several individual notes spaced about 0.2 seconds apart and sometimes lasting several seconds. The notes uttered during flutter-jumping are essentially the same as these individual long-cackle sounds. Lehmann (1941) has listed several variants of these cackling calls and combinations of *pwoik* and cackling notes, and he also mentions several other notes. These include calls sounding like *kwiee, kwerr, kliee, kwoo,* and *kwah.* In

the absence of comparative study and sonagraphic analysis, their possible functions cannot be guessed. Hjorth (1970) has noted that between flutter-jumping or booming the male often utters an indefinite staccato cackle, and during territorial confrontations it may produce cackling sounds that range from whinnies to whining cackles and explosive cackling sounds.

*Nesting and Brooding Behavior*

Following mating, the female begins to lay a clutch almost immediately; indeed, it is probable that she has already established a nest scrape prior to successful copulation. She may move a considerable distance away from the ground to her nest site and may actually nest nearer to another booming ground than to that at which copulation occurred (Robel et al., 1970). Robel et al. found that females had to visit a ground for an average of three consecutive days before copulation occurred, but did not return thereafter except perhaps for renesting attempts. Lehmann (1941) and Robel both found that renesting birds laid progressively smaller clutches, and sometimes up to two such attempts were made. The average clutch size of first clutches is about twelve to fourteen eggs for the lesser (Copelin, 1963), Attwater (Lehmann, 1941), and greater prairie chickens (Hamerstrom, 1939; Robel et al., 1970). Later clutches, probably the result of renesting, often have only seven to ten eggs.

Eggs are laid at the approximate rate of one per day, with occasional lapses of a day, so that it may take about two weeks to complete a clutch of twelve eggs (Lehmann, 1941). Incubation may begin the day before the laying of the last eggs or several days after the last egg is laid, according to Lehmann. Apart from two feeding and resting periods in early morning and late afternoon, the female incubates constantly. The incubation period is probably 23 to 26 days in all three forms (Lehmann, 1941; Schwartz, 1945; Coats, 1955; W. W. Lemburg*).

The process of pipping may require up to forty-eight hours, during which the female appears highly nervous and the nest is apparently extremely vulnerable, because of the noises made by the chicks and the odors of the nest (Lehmann, 1941). Normally, the nest is deserted within twenty-four hours after the last chick is out of its shell. Females with young chicks typically perform decoying behavior with heads held low and wings drooping and nearly touching the ground, uttering a low *kwerr, kwerr, kwerr* (Lehmann, 1941). After the young are able to fly well, both the hen and brood typically flush when disturbed.

Chicks less than a week old may be brooded much of the time, possibly

*W. W. Lemburg, 1970: personal communication.

up to half the daylight hours (Lehmann, 1941). However, older chicks are brooded only at night, during early morning hours, and in inclement weather. Broods typically remain with females for six to eight weeks, when families gradually disintegrate. There is also considerable brood mixing, as when separated chicks join the broods of other females, even if the young are of different ages.

## EVOLUTIONARY RELATIONSHIPS

The close and clearly congeneric relationships of the pinnated grouse to the sharp-tail have already been mentioned in the account of that species. Thus, comments here will be restricted to the relationships among the four forms of pinnated grouse. Short (1967) has already dealt extensively with the criteria advanced by Jones (1964a) for considering the lesser prairie chicken as specifically distinct from the greater prairie chicken. Since then, Sharpe (1968) has found some male behavioral differences between the lesser prairie chicken and the two surviving races of *cupido*. These differences consist of acoustic differences (higher frequencies in the lesser), time differences (more rapid and shorter displays in the lesser), and some motor differences (one versus two tail movements during booming in the lesser). A few other contextual and orientational differences were also found, but Sharpe admitted that these differences may be attributed largely to size differences in the birds and possible selection related to aggressive behavior patterns rather than being the result of reinforcement for species differences during some past period of sympatry. He concluded that the lesser should be considered an "allospecies" to emphasize its greater difference from *T. c. pinnatus* than that exhibited by *T. c. attwateri*. This may well be the most effective way of handling questionable allopatric populations, but it is not used elsewhere in this book and has not been generally adopted.

It would seem that the living forms of pinnated grouse and those which have recently become extinct were all derived from some ancestral grouse associated with deciduous forest or its edge, since the original ranges of the lesser and greater prairie chickens as well as the extinct heath hen all had affinities with oak woodlands or oak-grassland combinations. The Attwater prairie chicken, on the other hand, is apparently associated with pure grassland vegetation. The separation of the ancestral stock of the lesser prairie chicken probably occurred during an early glacial period, and subsequent adaptation during postglacial times to an unusually warm and dry grassland habitat in the southwestern states has accounted for its smaller size and generally lighter coloration. More recent separation of

gene pools no doubt brought about the separation of the east coast (heath hen) and Gulf coast (Attwater) populations from the interior form, but the behavioral and morphological differences among these are minimal.