

# Pinnated Grouse

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*Tympanuchus cupido* (Linnaeus) 1758

*Other Vernacular Names*

Prairie chicken, prairie cock, prairie grouse, prairie hen; cupidon des prairies, poule des prairies (French); Eigentliche Präriehuhn (German).

*Range*

Currently resident in remnant prairie areas of Michigan, Wisconsin, and Illinois and from eastern North Dakota and northwestern Minnesota 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.

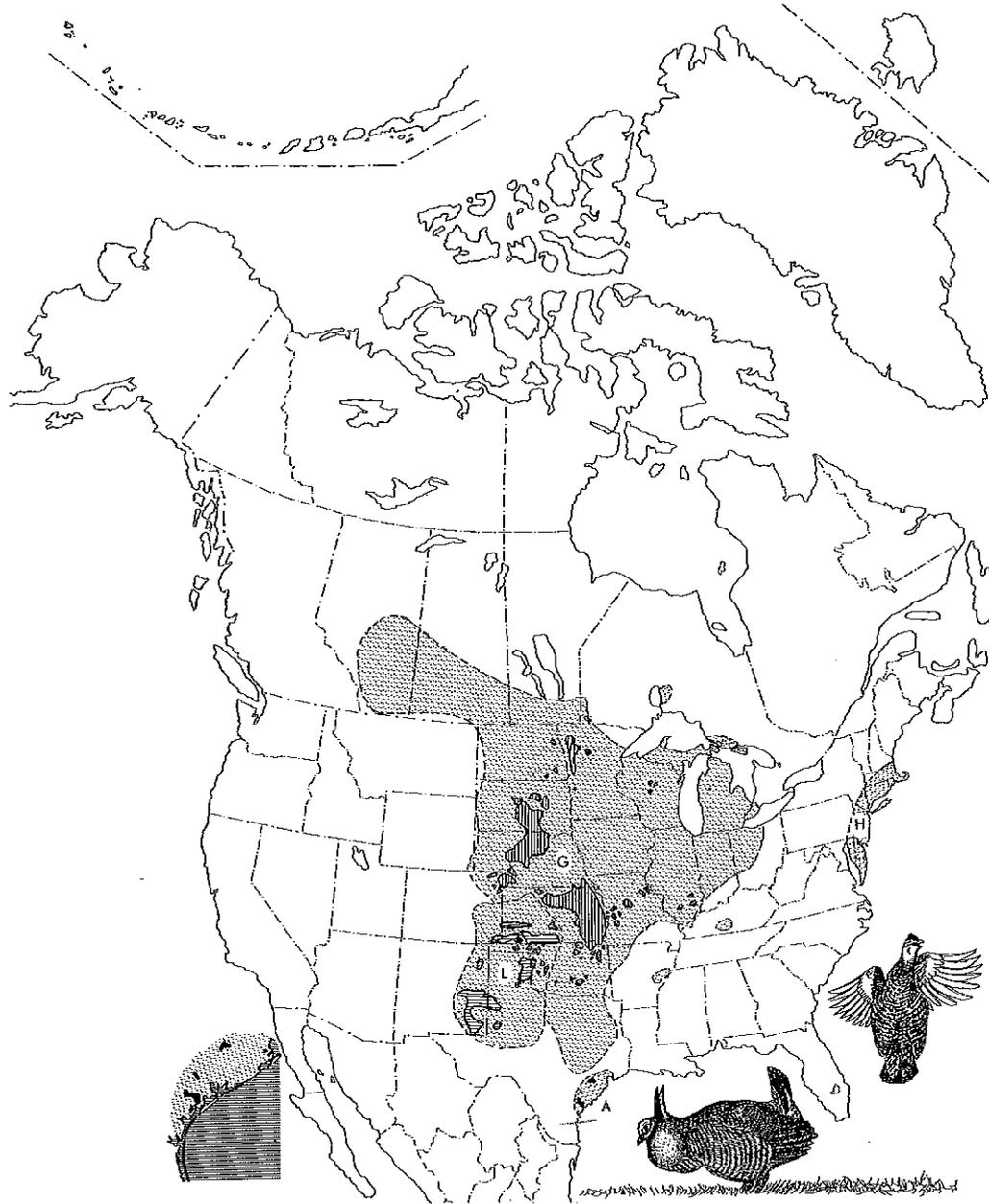
*Subspecies*

*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 (nearly extirpated), Wisconsin, and Illinois and to the grasslands of northwestern Minnesota, eastern North Dakota, South Dakota, Nebraska, Kansas, western Missouri, and northern Oklahoma.

*T. c. attwateri* Bendire: Attwater prairie chicken. Currently limited to a few isolated populations along the coast of Texas from Aransas 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.



14. Current distribution of the Attwater (A), greater (G), and lesser (L) races of the prairie chicken, and the original distribution of the heath hen (H). The inset map shows the current (1979) Texas range of the Attwater prairie chicken, and the stippling indicates the historic ranges of all forms of pinnated grouse.

## 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. The two sexes are nearly identical in plumage. The tail is short and somewhat rounded and the longer under (but not upper) tail coverts extend to its tip. The necks of both sexes have 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 the 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 crossbars, 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 pinna 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* of the greater prairie chicken are scarcely separable from those of the lesser prairie chicken (see that account) and also resemble young sharp-tailed grouse. However, prairie chickens have a somewhat more rusty tone on the crown and the upperparts 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 under tail 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* 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 by providing acorns as winter food (Sharpe 1968). 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 6 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*-*Andropogon*) 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 strongly 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 of 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 where these habitat needs could no longer be met, 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 I will attempt 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 was extirpated from Louisiana by 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 populations suffered from a badly distorted sex ratio, intensified farming practices, predators, fire exclusion, pesticides, and bad drainage practices, and relatively little area was 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 was a critical step toward retaining viable 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 a summary of the status of this bird in the late 1960s. 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. By the late 1970s the population was estimated at about 2,000 birds, with the largest populations in Aransas, Refugio, and Goliad counties, a secondary population in Austin and Colorado counties (Attwater's Prairie Chicken National Wildlife Refuge), and a third population on private rangelands in Victoria County (Kessler 1979). As of 1980 the total population was estimated by Lawrence and Silvy (1980) at 1,584 birds, or up 48 percent from 1967. These authors indicated that the population is now centered on about 120,400 hectares (75 square miles) of potential range, with 53 percent in Aransas, Goliad, and Refugio counties, 32 percent in Austin and Colorado counties, 6 percent in Galveston County, 4 percent in Victoria County, and the remaining 5 percent in Fort Bend and Brazoria counties. They judged that the total population should remain stable for the next decade, given no unpredictable catastrophes, though remnant populations in Galveston and Brazoria counties are likely to disappear. About 10 percent of the population is on refuge lands in Colorado and Aransas counties, and the rest is on private lands.

The present range of the lesser prairie chicken centers in the panhandles of northern Texas and northwestern Oklahoma, but it also includes parts of southwestern Kansas,

southeastern Colorado, and eastern New Mexico. In Oklahoma the present range includes several isolated populations spread over about 1,090 square miles (2,800 square kilometers), and contained about 7,500 birds in the spring of 1979. There has been a loss of more than half of the population's range in twenty years, and an approximate reduction of the population by half since 1944 estimates. The largest remaining populations are in Beaver, Ellis, and Woodward counties, with much smaller numbers in Beckham, Harper, Roger Mills, Texas, and Woods counties (Cannon and Knopf 1980). Hunting is still allowed in the state, and the 1979 harvest was estimated at 134 birds.

In Texas lesser prairie chickens have likewise been in a long-term declining trend, and the estimated fall population in 1979 was between 11,000 and 18,000 birds. After thirty years of protection, hunting was first allowed again in 1967, and since that time a few hundred birds have been taken annually. The 1979 harvest was probably about 600 birds (Crawford 1980). The occupied range is about 4,625 square kilometers (Taylor and Guthery 1980).

The third of four states where the lesser prairie chicken is sufficiently abundant to be legally hunted is Kansas, where the estimated fall 1979 population was 17,000 to 18,000 birds and the harvest was about 2,900. There too the population is declining (Crawford 1980). Its habitat is diminishing at the rate of 1.5 to 6 percent annually, largely because of the effects of center-pivot irrigation (Waddell and Hanzlick 1978). The occupied range is about 778 square kilometers (Taylor and Guthery 1980).

New Mexico is the other only state that currently allows the hunting of lesser prairie chickens. Its estimated fall 1979 population was some 10,000 birds, and about 1,200 birds were legally shot that year. Since 1960 the birds have been legally hunted, and harvests have generally been about 1,100 birds per year. Its population in that state is apparently stable and is essentially limited to five counties, centering on Roosevelt County (Sands 1968). The occupied range is about 18,898 square kilometers (Taylor and Guthery 1980).

Besides these four states, there is a small population in Colorado that probably numbered 400 to 500 in the fall of 1979. It is considered a threatened but stable population and is protected from hunting (Crawford 1980). It has probably benefited from such protection; Hoffman (1963) reported a substantial increase of males on censused display grounds between 1959 and 1962. The occupied range is about 1,634 square kilometers (Taylor and Guthery 1980).

Beyond these states, the lesser prairie chicken has been extirpated from Missouri (where it is known only from nearly century-old winter records) and is considered hypothetical in Nebraska (where it may have once occurred in the extreme southwestern corner of the state). It was released on the island of Niihau, Hawaii, during the 1930s, but its present status there is unknown (Crawford 1980).

Crawford (1980) estimated the total fall 1979 continental population as 44,400 to 52,900 birds, and generally it is either stable or declining. The species' range of about 27,300 square kilometers has decreased by more than 90 percent in the past century, and there has been a 78 percent decrease in range since 1963 (Taylor and Guthery 1980). These authors estimated a current population of 46,700 to 55,330 birds.

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 its prior range in the Canadian provinces (Hamerstrom and Hamerstrom 1961). Westemeier (1980) 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 were seen as late as 1960 (Stempel and Rogers 1961). The estimated population in Indiana diminished from more than 400 males occupying 33 booming grounds in 1942 to 4 males on a single booming ground by 1966. Christisen (1969) indicated a current estimated total Indiana population of only 10 birds in 1968, but by 1979 the population was considered extirpated.

Similarly, although Michigan may have had a population of about 200 birds in 1968, by 1979 there were fewer than 50 (Westemeier 1980). In 1980 the estimated number was only 20 birds, which were limited to a section and a half of publicly owned grassland (*Nebraskaland*, September 1980, p. 35).

In Illinois the estimated population dropped from 300 to 230 birds between 1968 and 1979, but in 1980 the spring count was up to 334 birds. These occur on some 1,640 acres of grassland that is being specifically managed for prairie chickens, so their population is probably secure. About 1,000 of these acres are in Jasper County, and the remainder are in Marion County. Additional very small remnant flocks occur in Washington and Wayne counties, not on protected lands (Westemeier 1980; in litt.).

In Wisconsin the population shifted from about 1,000 birds in 1968 to an estimated 1,842 in 1979 and appears to be increasing. In central Wisconsin about 100 square kilometers (39 square miles) are being managed for the species, and a reintroduction attempt will be made on the Crex Meadows Wildlife Area (47 square miles) of northwestern Wisconsin (Westemeier 1980). Hunting was last permitted in 1951.

In Minnesota, however, the estimated populations declined from 5,000 birds in 1968 to about 2,000 in 1979. These birds occur on about 78 square miles (about 200 square kilometers) of habitat, and in 1977 they were apparently successfully reintroduced in the Lac Qui Parle Wildlife Management Area, which would increase their available habitat somewhat (Westemeier 1980). Hunting was last permitted in 1942.

In Missouri the prairie chicken population was approximately 9,600 birds in 1979, or nearly the same as the same as the 10,000-bird estimate of 1968. These are distributed on some 900 square miles of range, most of which is in public ownership and is being managed specifically for prairie chickens. Hunting has not been allowed since 1906.

In North Dakota the total 1979 population was estimated at some 1,000 birds, which occur on about 220 square miles of habitat. In 1969 the estimated state population was about 1,800 birds, but locally the populations may have increased recently because of better management of federally owned grasslands by the United States Forest Service (Westemeier 1980). The last legal hunting season was in 1945.

In Colorado the population has declined from an estimated 7,600 in 1968 to between

300 and 3,000 in 1979. The total range of greater prairie chickens in the state is about 430 square miles and is currently declining as a result of grassland losses to center-pivot irrigation and row-crop farming (*Nebraskaland*, September 1980, p. 35). Plans are now under way to restore the South Platte Management Area to conditions suitable for prairie chickens, and to reintroduce them there (Westemeier 1980). Hunting was last allowed in 1937.

These seven states must all be considered relatively marginal, and they collectively support fewer than 20,000 birds at present. Most of the greater prairie chicken's population is to be found in Oklahoma, Kansas, Nebraska, and South Dakota.

In Oklahoma the total greater prairie chicken population was estimated at about 8,400 birds in the spring of 1979. These were distributed over 2,400 square miles (6,100 square kilometers) in thirteen northeastern counties, with the largest populations in Osage and Craig counties. Since 1943 there has been a 42 percent decrease in occupied range and a 34 percent decline in actual numbers. The Oklahoma population includes a fairly stable western component and a rapidly declining eastern one (Martin and Knopf 1980). The population is currently hunted, with an estimated 1979 harvest of 4,971 birds (Mark Byard, in litt.).

The South Dakota population of prairie chickens is in the vicinity of 40,000 birds, or half of that estimated to be present in 1968 (Westemeier 1980). The birds are distributed over an area of about 14,000 square miles, and the population is probably declining as a result of recent droughts, plowing of rangelands, and heavier grazing pressure. The state has a regular hunting season lasting approximately 80 days, and in 1978 an estimated 5,233 birds were legally taken. The highest populations occur in Jones County, where native grasslands occupy about 68 percent of the land area and cultivated lands about 30 percent; woody cover in South Dakota's prairie chicken range covers less than 1 percent of the total area (Janson 1953).

In Nebraska the greater prairie chicken 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 close by and provide both summer and winter habitat needs (Johnsgard and Wood 1968). The state's population is relatively static, and both this species and the more common sharp-tailed grouse have been regularly hunted, except in the case of the small and isolated population of this species in southeastern Nebraska, which is an extension of the large Flint Hills population of eastern Kansas. In 1967 the Nebraska harvest was estimated at 15,000 birds, and the state's total population in 1968 was estimated at 100,000 birds (Christisen 1969). In 1980 the total state population was placed as 75,000 to 100,000 birds, and the occupied range at approximately 7,000 to 10,000 square miles. The population is thus apparently stable, but increasing row-crop agriculture may bring about future declines. Between 1965 and 1968 the area of irrigated croplands in sixteen sandhills counties increased from about 26,000 hectares to 214,000 hectares, and there was a

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concurrent decline in the number of active prairie chicken leks (Robertson 1980). The usual annual harvest is between 10,000 and 30,000 birds, taken over an approximate fifty-day season (*Nebraskaland*, September 1980, p. 35).

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 area 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 50,000 birds were conservatively estimated to be present in the state (Baker 1953). In 1967 some 46,000 birds were harvested, and an estimated 750,000 were believed present in the late 1960s (Christisen 1969), suggesting that the Kansas population was by far the most secure of any state's. Yet by 1979 the estimated population had declined to 200,000 birds (Westemeier 1980). Although rural mail carrier surveys between 1963 and 1980 indicate recent downward population trends, booming-ground counts have indicated a generally upward recent trend, and the latter seem to correlate better with hunter harvest data (Rogers Wells, Prairie Chicken Population and Harvest Summary, 1979, Federal Aid Project no. W-23-R18). The 1979 estimated hunter kill was 88,400 birds, the highest since 1959 and well above the recent state average of about 34,000 birds.

In summary, it seems that the total collective fall populations for the three extant prairie chicken forms might be about 1,500 for the Attwater, about 50,000 for the lesser, and about 500,000 for the greater. Of the three, the endangered Attwater has remained stable or increased somewhat, the lesser has likewise remained stable in its most important population centers but has declined locally, and the greater has exhibited a probable population decline of about 50 percent in about a decade. However, the areas of apparently greatest decline (South Dakota, Oklahoma, and Kansas) are the ones where the population estimates have often been based on limited information, and in Kansas and Nebraska the population may actually be fairly stable. Correlated with the population decline there has been an approximate 28 percent reduction in hunter kill since the fall of 1967 (Westemeier 1980). During the same period the species was extirpated from at least one state (Indiana) and is nearly gone from another (Michigan). Its survival in Wyoming (where it had been limited to Goshen County) is dubious, and it is probably also now gone from Manitoulin Island, the mainland of southern Ontario, and southern Manitoba. Only in Wisconsin, where a great deal of money is being invested in land purchase and management, does the species seem to be increasing at present.

## 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  $3\frac{1}{2}$  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 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 that Attwater prairie chickens 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 use of cultivated grains increased, 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 are an important part of present-day prairie chicken habitat, with corn providing the best winter habitat, provided 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 the birds can reach them 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 primary foods during winter. Martin, Zim, and Newlson (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 birch, aspen, elm, and hazelnut among items used in the northern range during winter, but as long as grain or other seeds are available this does 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 near the extensive and lightly grazed grasslands of the larger cattle ranches, providing a combination of available food and grassy roosting cover.

According to a summary by Taylor and Guthery (1980), the lesser prairie chicken uses grass cover for nearly all winter activities, with dwarf half-shrubs also being used as roosting cover. Sites having Harvard oak (*Quercus harvardii*) are also used during winter, perhaps for acorns, and crop plants such as sunflowers and sorghum are sometimes also important fall and winter food sources. In the Attwater prairie chicken the clumped midgrass cover type is apparently a preferred type throughout the year (Horkel 1979).

#### *Spring Habitat Requirements*

The habitat requirements of the lesser prairie chicken for display grounds have been summarized by Copelin (1963). He reported that the males always selected areas with fairly short grass and that the grounds were usually on ridges or other elevations. In sand sagebrush habitat, on the other hand, display grounds were in valleys on short-grass meadows if the sagebrush on adjacent ridges was tall and dense. A variety of studies has indicated that this subspecies favors display areas that are nearly devoid of vegetation and provide excellent visibility. In west Texas 12 of 14 leks were on open areas created by humans, while the other 2 were on slightly elevated terrain where Harvard oak was 10 to 20 centimeters tall (Taylor and Guthery 1980).

Of several hundred Attwater prairie chicken booming grounds, most were on level ground, but they typically consisted of a short-grass flat, about an acre in extent, surrounded by heavier grassy cover (Lehmann 1941). Horkel (1979) reported that, of 24 sites he studied, 20 were in artificially maintained areas such as pipeline rights-of-way or roads.

Ammann (1957) has provided similar observations for the greater prairie chicken in Michigan. He noted that of 65 prairie chicken and 95 sharptail display grounds observed, 47 percent were on elevated sites and only 4 were in depressions. Of 97 Michigan prairie chicken grounds studied in 1941, 27 contained some woody growth other than sweet fern or leather leaf, while of 65 grounds studied since 1950 only 2 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.

Comparing habitat requirements of greater and lesser prairie chickens, Jones (1963) found that both forms preferred level or elevated sites with short grasses. Plant cover differences were not significant, but the 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 6 inches tall for their booming grounds, the combination of short cover and wide horizons apparently being far more important than specific cover type.

#### *Nesting and Brooding Requirements*

Ammann (1957) indicated that of 13 prairie chicken nests found in Michigan, 8 were in hayfields, 1 was in sweet clover, 3 were in wild land openings, and one was on an airport. All the nests were in fairly open situations. Hamerstrom (1939) has similarly reported on 23 prairie chicken nests in Wisconsin. Eleven of these were in grass meadows near drainage ditches, 3 were in dry marshes or marsh edges, 3 were in openings of edges of jack pine-scrub oak woods, 3 were in scattered mixtures of brush, small trees, and grass, 2 were in small openings in light stands of brushy aspen or willow, and 1 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 emphasized the importance of mixed natural grasslands or substitutes in the form of redbud (*Agrostis alba*) plantings as nesting and rearing cover types for prairie chickens. Yeatter (1963) correlated a decline in redbud production and prairie chicken

populations in Illinois and found that birds nesting in redtop had a nesting success as high 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 57 nest locations, 56 percent were in ungrazed meadows. Half of 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 (1945), Hamerstrom (1939), and Jones (1963) to comment on this relation. However, Robel et al. (1970) found considerable movement between booming grounds by females and questioned whether the location of booming ground has any major influence on female nesting behavior. He found that 19 nest sites average 0.68 mile from display grounds and ranged up to 1.13 miles away. Jones (1963) noted that all of the 9 greater prairie chicken nests he found were near pastures or old fields that had a large number of forbs into which the broods were taken after hatching.

Lehmann (1941) reported that of 19 Attwater prairie chicken nests found 17 were in long-grass prairie, one was in a hay meadow, and one was in a fallow field. All of them were in the previous year's grass growth, and 15 were in well-drained situations, often on or near mounds or ridges. Twelve were near well-marked trails, such as those made by cattle. All the nests were roofed over with grassy vegetation, and most had good to excellent concealment. Copelin (1963) reported on 9 lesser prairie chicken nests in Oklahoma and Kansas. None of these were among shrubs more than 15 inches high, and 7 were between grass clumps, particularly little bluestem (*Andropogon scoparius*). Two were under bunches of sage, and 1 was under tumbleweed. Shin oak shrubs from 12 to 15 inches tall were associated with 5 of the nests.

After hatching, females with broods typically moved to somewhat heavier cover than they used for nesting. Copelin (1963) noted that only 1 brood of lesser prairie chickens was found in the low shinneries of oak, but 27 were seen in oak motts, which are clumps of oak 4 to 20 feet tall in stands up to 100 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, which gives a combination of shade, protection, and easy movement. 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 1905; Schwartz 1945). Judd indicated that the prairie chicken eats only about half as much mast as does the ruffed grouse, the mast 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 I noted earlier, corn and sorghum are major winter foods for the species, with corn more important in northern areas and sorghum increasing in 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 eaten 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.

Year-round, Judd (1905) 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 the animal portion may reach 30 percent during summer 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 constituting more than 50 percent of the materials eaten. In contrast to the high percentage of cultivated grains noted 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 ruelli (*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 250 miles apart. The percentage of insects eaten was much higher for the lesser prairie chicken (41.8 and 48.6 percent average yearly volume in two habitats) than for the greater prairie chicken (8.2 and 20.8 percent average volume in two habitats). The rest of the food of both species consisted of seeds and green vegetation, with the latter usually greater in volume than the former. Both species fed in grassy cover, but whereas the lesser prairie chickens preferred midlength grasses for foraging, the greater were 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.

More recent studies of the lesser prairie chicken in New Mexico tend to confirm the results of Jones's study in Oklahoma (Davis et al. 1979, 1980). In New Mexico insects make up most of the summer diet, with chicks and young juveniles eating almost nothing but insects and even adults using mostly insects for their summer food. Spring foods in New Mexico are mainly green vegetation, especially the catkins of shinnery oaks or their acorns. Shinnery oak alone provides the most heavily utilized food source for the species throughout the year, and it is also the preferred concealment cover for foraging birds of all age-classes during the summer.

### 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 there was little movement 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 29 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 were by females; 6 of the 8 females recovered had moved at least 3 miles, while 18 of 30 males had moved less than 3 miles.

During winter, prairie chickens typically occur in large packs formed by mergers of the fall packs. In Wisconsin these can consist of 100 to 200 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' study area were often from  $\frac{1}{4}$  to  $\frac{1}{2}$  mile from feeding fields and were seldom more than  $1\frac{1}{4}$  mile away.

By February the winter packs begin to break up and the males start returning to their booming grounds. The Hamerstroms found that most of 56 banded males moved less than 2 miles from their winter feeding grounds to their booming grounds (50 birds), while the remaining males moved from 2 to 8 miles. Apparently many males winter at the feeding sites nearest their booming grounds, and in late winter some daily movements between these locations may occur. During spring males move little; they may roost on their territories or within a few hundred yards of them. Sources of water, shade, dusting places, and loafing sites are often within  $\frac{1}{2}$  mile. After display is over, 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 39 adult males, 37 adult females, and 31 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 largely between display grounds as the birds unsuccessfully attempted to establish territories at various grounds. During April and May both adults and immatures moved less, the birds remaining closely associated with specific booming grounds. Females moved most in April, during the time of peak male display. Females often visited several booming grounds, with movements of up to 4.8 miles recorded. One female that attempted to nest three times was fertilized at a different booming ground before 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 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, 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. Of 114 banded birds retrieved, 79 percent were found within 2 miles of their point of capture, and 97.4 percent were within 4 miles. The maximum known movement was 10 miles. In common with the Hamerstroms' study, Copelin found that juveniles often moved considerable distances between their brood ranges and display grounds used the following spring, with all of 14

birds moving at least 0.5 mile and 2 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 mile, and 20 adult males moved an average of 0.46 mile; 6 juvenile hens moved an average distance of 2.12 miles, and 1 adult hen moved 3.75 miles.

Lehmann (1941) provided some observations on seasonal movements in the Attwater prairie chicken that in general support the studies already discussed. He noted a summer movement of adults 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. During this time large concentrations of up to 250 to 300 individuals were sometimes seen, in addition to many smaller flocks of 8 or fewer birds. These winter packs broke up late in January, when males began to display.

More recent radio telemetry studies of the Attwater prairie chicken (Horkel 1979) indicate that average monthly ranges of males of this population varied from 28 to 211 hectares, with the largest ranges associated with the fall and winter booming periods and the minimum ranges associated with the nesting and brooding periods. Average monthly ranges of females varied from 35 to 267 hectares, with maximum ranges associated with the winter booming period and minimum ranges associated with the brooding season. Daily movements were estimated to range from 0.12 to 0.56 kilometer for males and from 0.13 to 0.46 kilometer for females.

In a similar radio telemetry study of the greater prairie chicken, Svedarsky (1979) found that females tended to return each spring to the booming ground on which they were trapped the preceding year, and that two females returned to nest within 30 meters of their previous year's nest site. During the first 2 weeks after hatching, broods moved approximately 2,000 meters per week.

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 number of males present averaged 13.7 and reached as high as 43. These grounds occurred on a study area of 16 square miles, and in different years from as few as 8 to as many as 40 display grounds were found there. The average figure of 24 display grounds indicates that good lesser prairie chicken habitat might support about 1.5 active display grounds per square mile. Taylor (1980) found 14 leks in an area of 5,200 hectares (20 square miles), or an average of 0.7 lek per square mile. These leks were separated by an average of 1.2 kilometers (0.74 mile). By comparison, Baker (1953) indicated that 6 greater prairie chicken booming grounds were present on a study area of 3.5 square miles of excellent range in Kansas, or 1.7 grounds per square mile. However, studies such as that of Sisson (1976) in Nebraska suggest considerably lower display ground densities of from 0.04 to a maximum of 0.53 per square mile. In general there thus seems to be a greater scattering of display grounds for the greater prairie chicken, which may in part

reflect the effective acoustical distances of 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 of display grounds.

## REPRODUCTIVE BEHAVIOR

### *Territorial Establishment*

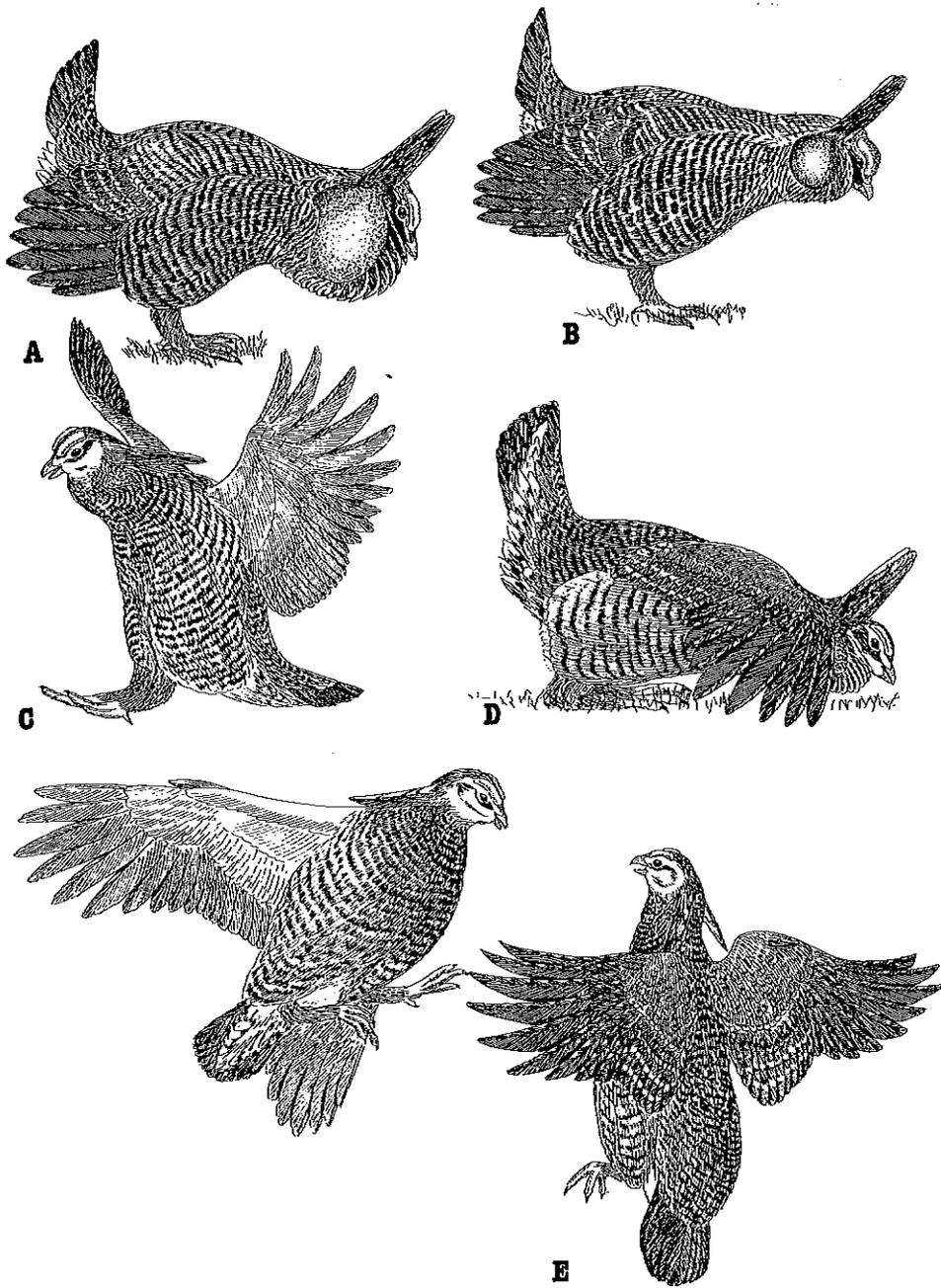
As in the sharp-tailed grouse, fall establishment of territories and associated display occurs regularly in the pinnated grouse. Copelin (1963) noted that during the fall old male lesser prairie chickens reestablish territories they held during the spring, and although young males visit the booming grounds they are apparently not territorial. In the greater prairie chicken an active period of fall display is likewise usual, 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 that young males learn the locations of these display grounds. During the following spring some shifting about may occur as winter deaths among the males 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 in sharp-tailed grouse. Lehmann (1941) indicated that for 5 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) found that on 17 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.

Of 610 booming grounds observed in Wisconsin between 1950 and 1971, 36 percent had between 1 and 5 birds, 34 percent between 5 and 10 birds, 19 percent between 10 and 15 birds, 8 percent between 15 and 20 birds, 2 percent between 20 and 25 birds, and 1 percent more than 25 birds (Hamerstrom and Hamerstrom 1973). Before experimentally manipulating lek composition, Ballard and Robel (1974) found that the average size of 13 territories was 152 square meters.

### *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, based on Sharpe's comparative analysis of the three forms (1968).



30. Male displays of pinnated grouse (after various sources), including booming by (A) greater prairie chicken and (B) lesser prairie chicken, (C) flutter-jumping of greater prairie chicken, (D) bowing by greater prairie chicken, and (E) fighting by greater prairie chickens.

Booming is the collective term given to the sequence of vocalizations and posturing that greater prairie chicken males use both to announce territorial residence to other males and to attract females. During booming, the tail is elevated, the pinnae are variably raised until they may be almost parallel with the ground, the wings are lowered while held close to the body, and the primaries are somewhat spread. 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, then he snaps his 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 2 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 later tail-spreading elements are lacking. He estimated that maximum amplitude of the fundamental harmonic during booming at 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 prairie chicken lasts about 0.6 second, as opposed to nearly 2 seconds in the greater. The associated call ("yodeling" 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 that 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 antiphonally ("duetting" of Hjorth 1970), performing up to ten displays in fairly rapid sequence. An additional visual difference between the displays of the two forms is that the exposed gular sac of the lesser prairie chicken 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 those of the sharptail, however, most prairie chicken flutter-jumps have associated cackling calls ("jump-cackle" of Hjorth 1970). Sharpe (1968) found that calls occurred during 27 of 30 flutter-jumps in Attwater prairie chickens, 16 of 20 in lesser prairie chickens, and 17 of 20 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, males typically use several display postures and calls. Ritualized and actual fighting, such as Lumsden (1965) described for the sharp-tailed grouse, is commonly seen, often including 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 sharptails, and a 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. He performs booming with high frequency as well as extreme posturing, particularly pinnae erection and eyecomb enlargement. The eyecombs 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 the Attwater prairie chicken. Between booming displays, the male will sometimes stop and “pose” facing the female, but most booming displays are not oriented specifically toward the hen. Rather, the male circles her, and all aspects of his plumage are visible to her.

In the presence of females, 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 the Attwater prairie chickens, but in the lesser it is higher pitched and sounds like *pik* (“squeak” of Hjorth 1970). It is shorter (0.23 second compared with about 0.4 second 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 erect. 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, the male grasps the female's nape, lowers his wings on both sides of her, and quickly completes 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.

Ballard and Robel (1974) found that, of 132 attempted copulations they observed before manipulating lek composition, 92 percent were successful, and 89 percent of these were performed by dominant (alpha or beta) males. After the dominant males had been eliminated, only 13 percent of 39 attempted copulations were successful. These were performed by males of lower social status that had moved into the center of the lek after the dominant birds were removed. Not only did removing these dominant males disrupt the social organization of the lek during the year when it was done, but similar effects carried

over to the following spring. Thus, during the next year there were fewer males on the lek, fewer females visited it, and fewer successful copulations were observed (Robel and Ballard 1974). Not only did these authors confirm a well-developed and experience-related social hierarchy among males, but they also noted that females varied in dominance status as well. One undesirable result of such dominance behavior among females may have been to delay fertilization, and thus the onset of nesting, in some low-ranking females, thereby affecting nesting success rates.

Although Robel and Ballard thus effectively proved the importance of social structuring and the role of experienced males in regulating reproductive efficiency, it should be noted that Hamerstrom and Hamerstrom (1973) reported that 18 percent of 2,264 copulations were performed by first-year males, and that these young birds were apparently as successful in their copulation efforts as were adults (84 and 76 percent respectively).

#### *Vocal Signals*

In addition to the booming, whining, quarreling, and *pwoik* calls already mentioned, pinnated grouse have several other vocal signals, including many cackling sounds. Sharpe (1968) recognized a "long cackle" that consists of several individual notes spaced about 0.2 second 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*, *klee*, *kwoo*, and *kwah*. In the absence of comparative study and analysis, their possible functions cannot be guessed. Hjorth (1970) has noted that between bouts of flutter-jumping or booming the male often utters an indefinite staccato cackle, and during territorial confrontations he may produce cackling sounds that range from whinnies to whining cackles and explosive cackles. Sparling (1983) has provided a detailed recent sonographic analysis of the vocalizations of greater prairie chickens, sharp-tailed grouse, and their hybrids.

#### *Nesting and Brooding Behavior*

After mating, the female almost immediately begins to lay a clutch; indeed, it is probable that she has already established a nest scrape before successful copulation. She may move a considerable distance away from the display 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 3 consecutive days before copulation occurred but did not return thereafter except perhaps for renesting attempts. Lehmann (1941) and Robel et al. found that renesting birds laid progressively smaller clutches, and sometimes two such attempts were made. The average clutch size of first clutches is about 12 to 14 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 7 to 10 eggs. Svedarsky (1979) found an average clutch size of 14.6 eggs for initial nests, and an egg-laying rate of 1 per day, for

greater prairie chickens in Minnesota. He determined that egg laying began an average of 3.8 days after copulation, and that six females began second nesting efforts an average of 6.4 days after losing their initial clutches.

Nest sites that provide dense, vertically oriented cover may be important, as are habitats that have remained undisturbed for a year or longer (Svedarsky 1979). Incubation may begin the day before or several days after the last egg is laid, according to Lehmann (1941). 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; Svedarsky 1979). Svedarsky found an average period of 25.5 days, with slightly longer periods typical of early nests.

Judging from the work of Ballard and Robel (1974), nests that are initiated later in the season (May 5 or later in their study) not only have lower clutch sizes than earlier clutches (10.2 vs. 12.1 eggs), but also have a lower probability of successful hatching (10 percent vs. 44 percent). Somewhat higher nesting success rates were reported by Sisson (1976) for Nebraska (50 percent of 29 nests) and by Svedarsky (1979) for Minnesota (62.4 percent of 36 nests).

Pipping may require up to 48 hours, during which the female appears highly nervous and the nest apparently is extremely vulnerable because of the noises made by the chicks and the odors of the nest (Lehmann 1941). Normally the nest is deserted within 24 hours after the last chick is out of the 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 the brood typically flush when disturbed.

Chicks less than a week old may be brooded much of the time, possibly 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 6 to 8 weeks, after which 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 relation of the pinnated grouse to the sharptail has already been mentioned in the account of that species. Thus, comments here will be restricted to the relation 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 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 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 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 that it is more unlike *T. c. pinnatus* than is *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 appears that the living forms of pinnated grouse and those that 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.

# The Grouse of the World

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