

THE SPECIFIC DISTINCTNESS OF THE GREATER AND LESSER PRAIRIE CHICKENS

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SOME disagreement exists as to whether the Lesser Prairie Chicken (*Tympanuchus pallidicinctus*) and the Greater Prairie Chicken (*Tympanuchus cupido*) are distinct species or members of the same polytypic species. Aldrich and Duvall (1955: 8) have considered these birds to be conspecific, although without argument other than the statement: “. . . we find no characters that differ from those of the other prairie chickens, except in degree; thus, only a racial difference is indicated.” The A.O.U. *Check-list of North American birds* (1957), however, continues to agree with Peters (1934: 41), Ridgway and Friedmann (1946: 219), and earlier workers, and lists them as separate species.

The essentials of the past and present distributions of the prairie chickens are shown by Baker (1953: 5) and by Aldrich and Duvall (1955: 8-9). The Greater Prairie Chicken occupies, or has occupied, a wide, gradually changing, partially disjunct range in the eastern and central United States and is undramatically polytypic. Of the races *T. c. pinnatus*, *attwateri*, and *cupido*, the last (or “Heath Hen” of the north Atlantic coast) is extinct and *attwateri* is threatened with extinction (*Auk*, 80: 360, 1963). The Lesser Prairie Chicken occupies a comparatively small range to the southwest of the Greater, today occurring in eastern Colorado and New Mexico, western Kansas and Oklahoma, and northern Texas. It is monotypic.

While the morphological characters that separate the Greater and Lesser prairie chickens may differ only in degree, the degree seems greater to my eye than that separating the several races of the Greater Prairie Chicken, especially with regard to coloration and markings.

Since the study of behavior has already been used to throw light on the evolutionary trends in North American and European grouse, for example by Wing (1946), Scott (1950), and Hamerstrom and Hamerstrom (1960), the present study was undertaken with the hope that similarities and differences in courtship behavior, as well as in behavior through the remainder of the year, might help in assessing the validity of recognizing these two prairie chickens as distinct species. The data here presented have been obtained by observing the birds on the booming and feeding grounds, by flushing them from coverts, and by tracking them in the snow, sand, and mud.

BEHAVIOR

My observations were made from June through November, 1959, and from February, 1960, to September, 1961. Field stations were located on

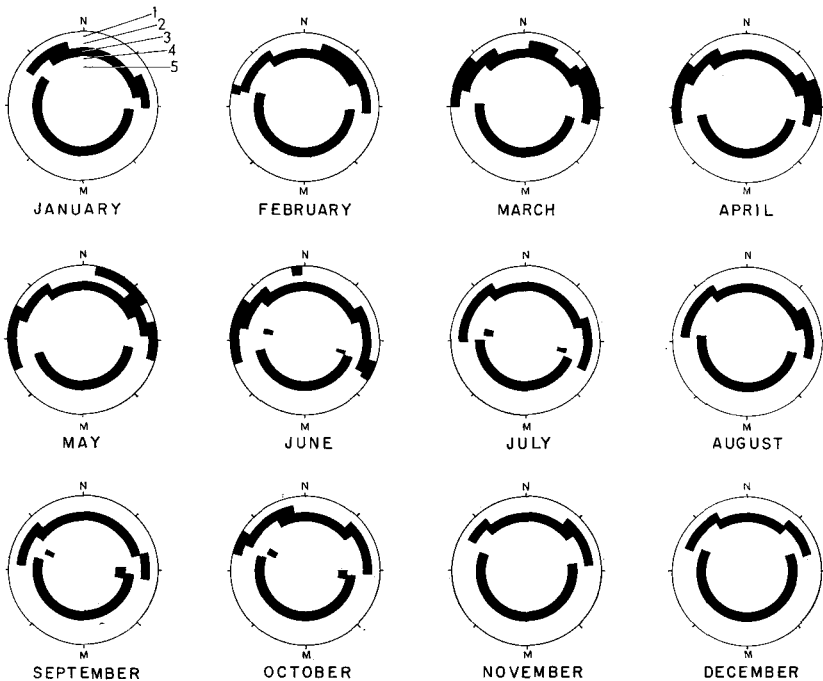


Figure 1. The change in patterns of activity of the Greater Prairie Chicken through the year, Osage County, Oklahoma. Circle 1, booming activities; circle 2, feeding activities; circle 3, resting activities; circle 4, night roosting; circle 5, watering activities ($N = 1200$ hours, $M = 2400$ hours).

the K. S. Adams Ranch, Foraker, Oklahoma, and the Maple Ranch, Beaver, Oklahoma. Alternate two-week observation periods were used in order to cover both forms equally. In the second year, the observation periods were reversed to coincide with the periods of non-observation of the first year. Hence, approximately one full year was spent with each kind of prairie chicken. Behavioral activities described below pertain to both forms unless specified.

COURTSHIP

Prairie chickens spend much time on their display grounds. One of the most conspicuous differences between the two kinds, however, was the difference in the amount of time so spent. Lesser Prairie Chickens were found on the courtship grounds (going through at least some of their courtship activities) in all months except August and December; Greaters were absent in December, January, and July through September (Figures 1 and 2 and Table 1).

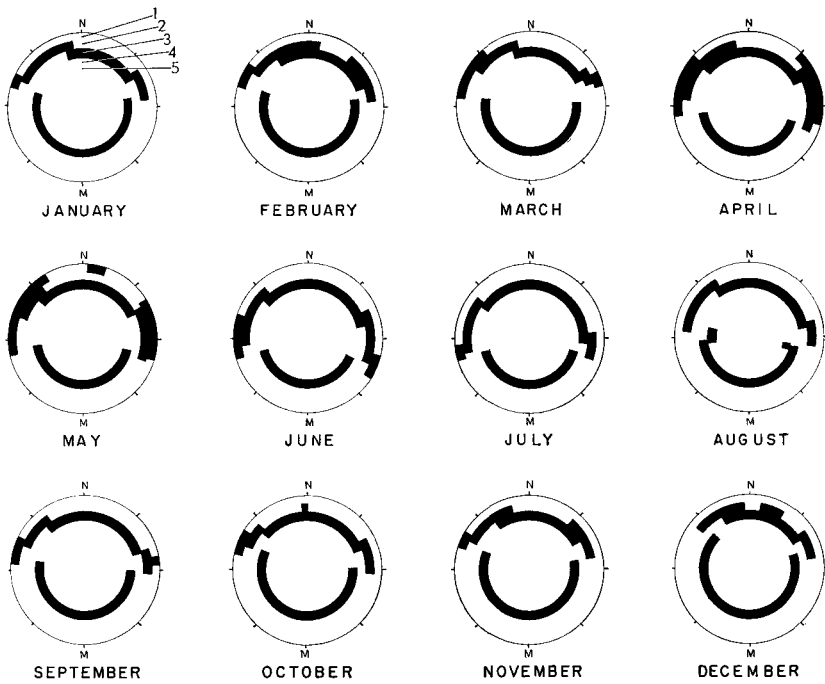


Figure 2. The change in activity patterns of the Lesser Prairie Chicken through the year, Beaver County, Oklahoma. Circle 1, booming activities; circle 2, feeding activities; circle 3, resting activities; circle 4, night roosting; circle 5, watering activities ($N = 1200$ hours, $M = 2400$ hours).

During the year many changes take place in the reactions of the prairie chickens to one another. These are summarized in Table 1. To facilitate description of the birds' behavior, the year was divided into the precopulatory, copulatory, and postcopulatory periods. There was no clear-cut break between these periods.

Precopulatory period.—Chasing was the primary activity of the birds during the precopulatory period (Table 1). Very few birds were settled upon regularly-occupied territories. Fights between birds were irresolute, perfunctory performances rarely lasting a minute. The birds were extremely restless and seldom remained in one place very long. They were easily flushed by predators, and when flushed often did not return in the same morning to their individual courtship areas. The booming notes were weak in comparison with those heard during the ensuing copulatory period. Fall booming closely resembled that seen in the early spring and hence autumn behavior has here been considered as "precopulatory," along with that of early spring.

TABLE 1
COURTSHIP ACTIVITIES OF LESSER AND GREATER PRAIRIE CHICKENS BY MONTHS

<i>Month</i>	<i>Lesser Prairie Chicken</i>	<i>Greater Prairie Chicken</i>
PRECOPULATORY PERIOD		
January	Birds booming and chasing one another; chasing particularly strong.	Absent from booming grounds.
February	Very active; activity mostly chasing. Later in month much fighting.	Very active, booming, chasing, and fighting; very few sit quietly for long.
March	Very active; territories seem fixed; more fighting and chasing than in April.	Still very active; some birds settle down on definitely defended territories.
COPULATORY PERIOD		
April	Very active; rigorous fights; females present; copulation occurs.	Females present; copulation occurs.
May	Strong activity; copulation occurs.	Booming very active; less fighting and chasing than earlier.
POSTCOPULATORY PERIOD		
June	Activities on the booming grounds are primarily resting and preening.	Feeding on booming grounds begins earlier; birds spend much time preening; booming intermittent and weaker.
July	Occasional booming; resting and preening take up most of the birds' time.	Absent from booming grounds.
August	Absent from booming grounds.	Absent from booming grounds. Large groups of young birds sometimes seen "playing" and going through "courtship" actions elsewhere.
PRECOPULATORY PERIOD		
September	Much chasing, but fighting not rigorous. Birds closer together on booming area than in spring.	Absent from booming grounds.
October	Females present; activity primarily chasing; males chase females rather than display before them. Booming note weaker than in spring.	Birds present on booming grounds. Some fighting and leaping into the air; birds often chase one another. Booming consists of a single, clear note with muffled second note; very weak third syllable sometimes heard by end of month.
November	Fewer birds appearing on booming grounds; activities similar to those of October.	Absent from booming grounds. Some courtship activities in the large feeding flocks.
December	Absent from booming grounds.	Absent from booming grounds.

Differences in courtship activities of the two forms during the precopulatory period are summarized by months in Table 1. A notable difference was the greater amount of time the Lesser Prairie Chickens spent on the booming grounds in this period. Lessers were present during all six months designated as precopulatory, while Greaters were present in only three of these months.

Copulatory period.—The courtship behavior of the birds during the copulatory period resembled, more completely than that of the precopulatory period, the descriptions already given by Breckenridge (1929), Scott (1950), Hamerstrom and Hamerstrom (1960), and Schwartz (1945), the last of which is particularly detailed and all of which apply to the Greater Prairie Chicken.

As spring progressed, individual territories became more firmly established. Defense of these small territories increased and some birds fought more or less continuously during the entire morning's activities.

Dancing in both forms reaches its greatest intensity during the copulatory period. The most important difference between the two forms in this period is one I noticed between their dances. A characteristic component of the dance of both forms is a rhythmic stamping of the feet. Before stamping, however, the Lesser moved its wings, alternately, with the same rhythm as that of the stamp directly to follow. This wing movement before the stamp seems not to have been described in literature for the Greater Prairie Chicken, nor was it observed by me.

Postcopulatory period.—During the postcopulatory period little booming and fighting were seen. The booming note was weak and the little fighting done was desultory at best. While on the booming ground during this period the birds spent most of their time each morning resting and preening. This was the only time I observed either form preening.

Remarks.—With respect to the considerable difference noted in time spent by the two forms on the booming grounds, it may be conjectured that both forms require a certain amount of social contact. This, however, may be provided for the Greater Prairie Chicken by the large combined broods typical of the species in summer, and by the large feeding flocks of winter. For the Lesser Prairie Chicken, on the other hand, in which such aggregations are rare or lacking, social contact may be provided by meeting at the booming area.

OTHER ACTIVITIES

There seemed to be few differences between the two forms in time of feeding (Figures 1 and 2). The morning feeding period was somewhat longer for the Lesser Prairie Chicken, while both morning and evening periods were used about equally by the Greaters.

The two forms differed markedly in the time of day used for dusting. Dusting by Lesser Prairie Chickens was done in the morning and afternoon resting periods (observed between 0900 and 1030 hours and between 1530 and 1800 hours) of spring and summer. Greater Prairie Chickens dusted only in the summer and used the feeding periods (observed 0600–0700 and 1800–1900) for this purpose.

Night roosting of the two forms was similar, both as to time and kind of place used (Figures 1 and 2). Roosting prairie chickens were found singly or in groups of up to 12. Based on 81 observations for the Lesser and 36 for the Greater, the mean size of nightly roosting groups was 2.2 birds and 2.0 birds, respectively. Individual roosts were located from 1 to 20 feet apart.

Both Lesser and Greater prairie chickens used water in the late summer and fall. The birds were extremely cautious in approaching water sources.

The Lessers would fly to an elevation near a water tank (the sources of water for these birds were invariably stock tanks filled by windmills), then walk slowly to the tank. While they were drinking, however, they did not appear cautious. The birds would perch on the edges and lean over into the tank to drink. Usually excess water was available on the ground, but the birds did not use this, seeming to prefer the tank water. Not all birds drank when the flock came to water; some would feed actively or “play” near the water’s edge.

The Greaters fed in the vicinity of the stock ponds where they watered. They approached the water entirely by walking. Actions at the water were similar to those of the Lessers, although more feeding was done by the Greaters at this time.

OTHER DISTINCTIVE CHARACTERS

At the climax of the breeding season there is a striking difference in the color of the gular sacs of these two prairie chickens. For the Greater Prairie Chicken these sacs were adequately described by Schwartz (1945: 48) as follows: “The air sacs are a brilliant orange, narrowly edged with red which is more pronounced next to the pinnae.” Although the gular sacs of the Lesser Prairie Chicken were described by Ridgway and Friedmann (1946: 220) as yellow during the breeding season, I did not find this to be true. The gular sacs of the Lesser Prairie Chickens that I saw in the breeding season were a brilliant red, much the same as the color edging the orange gular sac of the Greater.

There is also an obvious difference in the booming notes of the two prairie chickens. The Lesser has a higher-pitched note than does the Greater, and this note has less ventriloquial quality in the former.

Lesser Prairie Chickens use a greater amount of insect food through the

TABLE 2
MAJOR CLASSES OF FOODS USED BY PRAIRIE CHICKENS IN PER CENT OF VOLUME*

<i>Species</i>	<i>Type of food</i>		
	<i>Seeds</i>	<i>Green vegetation</i>	<i>Insects</i>
Lesser Prairie Chicken	24.5	33.5	42.0
Greater Prairie Chicken	38.9	48.5	12.6

* Based on samples of 1129 (Lesser Prairie Chicken) and 990 (Greater Prairie Chicken) droppings taken in the two years of the study.

year than do Greater Prairie Chickens (Table 2). As might be expected, the species of the insect and plant foods utilized show a greater difference than do the major categories (Jones, 1963, and MS).

Habitat distinctions are also striking (see Table 3). Only the birds' relative use of plant life-forms is presented in Table 3, but distinctions were also detected in height, pattern, and composition of the plants used by the two forms of prairie chickens (Jones, 1963). The habitat difference of primary importance is the use of shrub and half-shrub life-forms by Lesser Prairie Chickens and, conversely, the use of tall grass, short grass, and intermediate life-forms by Greaters.

DISCUSSION

The differences in habitat preference just noted seem great enough to me to indicate that, if these two prairie chickens were sympatric in the geographical sense, they would still be subject to a considerable degree of (if not to total) ecological separation.

They are not now sympatric, of course, and absolute proof of species limits seems to be precluded by this lack of sympatry.

We shall perhaps never be sure of the precise distributions of these forms upon the arrival in North America of Caucasian man. It is by no means certain, however, that the two forms have always been allopatric; indeed, a considerable possibility that they were not seems to exist. The

TABLE 3
PLANT LIFE-FORMS UTILIZED BY PRAIRIE CHICKENS FOR VARIOUS ACTIVITIES

<i>Use</i>	<i>Lesser Prairie Chicken</i>	<i>Greater Prairie Chicken</i>
Feeding	Grass of intermediate height	Short and tall grass
Resting	Half-shrub and shrub	Tall and intermediate grass
Courtship	Short grass	Short grass
Nesting	Half-shrub and grass of intermediate height	Tall grass
Brood-range	Shrub and half-shrub with forbs	Forbs and short grass
Escape	Half-shrub and shrub	Tall grass and short grass

best summary of the scattered evidence for a degree of sympatry may be that of Baker (1953; 7-9), who has reviewed many old records (chiefly made, it must be stressed, outside of the breeding season) of Lesser Prairie Chickens in central and eastern Kansas (where the Greater has long occurred) and even to southwestern Missouri. According to Haecker, Moser, and Swenk (1945: 11), moreover, there are old Nebraska records. Most interesting, however, although certainly not scientific evidence, is the following statement, discovered by Baker (in Duck and Fletcher, 1945: 68), to the effect that: ". . . some early settlers in western Oklahoma recognized two kinds of prairie chickens in the same area, but occurring on different mating grounds. The 'booming and cooing kind' (greater prairie chicken) was found in the uplands, and the 'gobbling kind' (lesser prairie chicken) was found in the sandhills along water courses" (Baker, 1953: 7).

If these indications of sympatry are correct, they provide some evidence of the ecological isolation postulated above. Further, it would seem likely that the behavioral differences here noted, particularly the differences in the dance, the difference in booming note, and the color of the gular sacs (and perhaps others yet undetermined), might provide strong psychological influences in maintaining reproductive isolation of sympatric populations.

SUMMARY AND CONCLUSIONS

The differences in behavior and morphology here noted, between the Lesser and Greater prairie chickens, may be summarized as follows:

- (1) Lesser Prairie Chickens spend a greater portion of the year in booming activities.
- (2) There is a slight difference in courtship performances. A wing flutter is preliminary to the foot stamp in the dance of the Lesser Prairie Chicken, but not in that of the Greater.
- (3) Booming notes of the two birds differ slightly.
- (4) Lessers dusted while resting, while Greateres dusted only in the feeding period.
- (5) In the breeding season, the gular sac of the Lesser is predominantly red, while that of the Greater is orange.
- (6) Lesser Prairie Chickens depend more on insect food than do Greater Prairie Chickens.
- (7) The habitats of the two birds differ to an appreciable extent.

While the two forms are now allopatric, there is some evidence that they may not always have been completely so.

With all of these considerations in mind, it is not easy to conceive of the two prairie chickens as certainly, or even probably, conspecific. They differ in ways so numerous and diverse that they should be treated as separate species until and unless some proof of their conspecificity much more convincing than anything now available is forthcoming.

ACKNOWLEDGMENTS

This project was supported by an Oklahoma Cooperative Wildlife Research Unit Fellowship (Oklahoma Department of Wildlife Conservation, Oklahoma State University, and Wildlife Management Institute cooperating). I wish to express appreciation to Mr. K. S. Adams and Mr. Mark Mayo, on whose lands the investigation was carried out.

Thanks are due Mr. A. M. Stebler and Dr. F. M. Baumgartner for reviewing and criticizing this manuscript. The results reported here represent part of a dissertation submitted in partial fulfillment of the requirements for the Ph. D. at Oklahoma State University.

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