MATING BEHAVIOR OF THE SAGE GROUSE

BY JOHN W. SCOTT

Plates 15, 16, 17

THE unique, polygamous nature of Sage Grouse (*Centrocercus urophasianus*) society has been little understood, or even suspected. Until less than three years ago, the writer knew only three persons who had seen the act of mating. Many believed the Sage Grouse did not mate. Others, including one ranchman who had seen the birds gather on his place for forty years, asserted that the cocks coughed up the male elements on the strutting grounds while engaged in strutting, and that the hens wandered over the area and picked them up. According to Girard (Univ. Wyoming Publ. 3: 1–56, 1935), many hunters, ranchmen and others believe that the cocks spawn and that the hens pick up this spawn. Such crude explanations are based on misinterpretations of observed behavior. Consequently, the significance of behavior during the mating cycle has been incompletely understood. Under such circumstances, the writer felt it important to investigate the whole mating cycle.

Simon (Auk, 57: 467-471, 1940) has given an excellent and relatively complete description of the strutting and mating performance of the Sage Grouse, and has briefly reviewed the literature bearing on this subject. Our observations in this respect agree closely with those of Simon. The two areas studied are at the same latitude, about 260 miles apart, but differ somewhat in altitude, and the work of Simon was limited to four morning observations, made on April 5, 6, 7 and 8, 1940. Under these circumstances we noted minor differences, as, for example, that mating begins at a later date at the higher altitude, and we could find no evidence that the group of cocks surrounding the hens at a mating spot served to keep the hens together, as suggested by Simon. The differences are chiefly due to the fact that our observations were more extensive and more complete. We carried our study of the mating behavior through an entire mating cycle and worked out the social behavior of the groups of individuals composing a social organization of approximately 800 birds. The remarkable polygamous system that prevailed is described in this paper.

A tent was set up on a suitable spot in a strutting area late in the afternoon before the birds came in, usually between five and six o'clock. All provisions and equipment needed were taken into the tent and the tent was closed. Observation was possible in all directions through a window and flaps in the tent. We did not appear

outside the tent until all observations were complete. This usually occurred between seven and eight o'clock the next morning, but at an earlier hour late in the season. A 16 mm. movie camera with telephoto lenses was used to record significant behavior. Careful notes were kept and the time recorded. Frequently a flashlight was needed to distinguish the time. Later, enlargements were made of individual frames of the movie film to illustrate this paper.

In the spring of 1940, six strutting grounds were located, and twelve nights were spent in the field making observations. In 1941, the largest of these areas was selected for intensive study, and fifteen nights, between March 18 and June 12, were spent in the field, with one additional early morning observation.

YEARLY BEHAVIOR CYCLE

In midwinter, Sage Grouse bunch up in flocks that may include several hundred birds in a single flock. At this season the birds are found on sagebrush areas since the sagebrush leaves constitute their principal food. Both sexes live peaceably together and there is no apparent rivalry among the cocks. With the approach of spring, the mating cycle is initiated and there is an extraordinary change in behavior. This cycle lasts, on the Laramie Plains, from early in March to near the middle of June.

After impregnation during the mating cycle, the hens scatter over wide areas to nest, sometimes in small groups with nests not far apart if cover is exceptionally good, but usually separated widely from each other. After the eggs hatch, the hens with chicks tend to gather in areas where water and small insects are present. The hens lead and care for the young. In early fall, groups are formed, maternal ties are broken and, several weeks later, hens, cocks, and young are found mixed indiscriminately together.

After the mating cycle, the cocks break up into groups of small or moderate size and spend the summer in isolated and remote areas. At this season we have observed no indication of serious rivalry. Early in the fall, the cocks begin to congregate into larger groups and, some weeks later, are joined by the hens and young birds on the winter feeding areas. Such, in brief outline, is the yearly routine.

THE MATING CYCLE

The areas devoted to sexual activity may be termed 'strutting grounds,' since the strutting of the cocks is the most noticeable and characteristic type of behavior on such areas (Plate 15). The size of the strutting grounds varies from an acre to forty or more acres

in extent. The area studied in 1941 averaged over 200 yards in width and was approximately one-half mile in length. At the height of the season, this area accommodated over 400 cocks and a varying, lesser number of hens. The total number of hens visiting the area during the season could not be counted, but probably equalled the number of cocks, according to estimates.

The strutting grounds may be termed 'hereditary' in the sense that the same areas are used year after year. Indeed, the instinct to return to the same location is so strong that a public road passing through one area did not prevent the annual return; some of the cocks strutted on and across the road from where the main body of birds was located. Birds are known to come a distance of several miles. In 1941, some of those that assembled on the strutting area under observation must have travelled a distance not less than four or five miles, possibly seven to ten miles, though there was another strutting ground only two miles away.

Strutting grounds are usually open, flat areas covered with short grass, or open areas on gently sloping hillsides. Nearby sagebrush is usually sparse and low in form. The soil is usually a sandy loam, but may vary from an alkali flat with little grass to an open slope where the small amount of remaining soil is mixed with small rocks and gravel. Three of six areas observed were near water.

At the assemblies early in the season, there is much challenging and fighting, as well as strutting, by which locations are established and dominance is to some extent determined. Strutting by cocks is more noticeable when hens are in sight, but it may also arouse antagonism and result in a challenge to fight a nearby rival. With a warm, open season, strutting probably begins in the latter part of February. It is interrupted and may stop entirely during severe weather. Spasmodic strutting, usually involving only a few birds, has been observed during warm spells in November, December, January, and February.

The number of birds on one strutting ground depends upon the number in the vicinity, the advancement of the mating cycle, the proportion of sexes present, the influence of weather, and the influence of light from the moon. The presence of enemies, particularly the Golden Eagle, may also temporarily alter the number of birds present. The Sage Grouse fears the eagle more than any other enemy, including man. The only other enemy, the coyote, was observed three times on strutting grounds, twice just after daylight, and once at sunrise. Eight cocks were known to have been killed on this area.

Four of these were killed by striking a barbed wire fence that separated two portions of the strutting ground. Another may have been killed in the same way or by an eagle. From the location and appearance of fragments of three others, two were killed by eagles and one by a coyote. One cock that struck the barbed wire was knocked tumbling, but later limped away. Eagles flew over the area nine times on the sixteen mornings under observation, three times one morning.

On the area under observation, some of the cocks began to assemble on the strutting ground early in March. On the cold, gray morning of March 20, after one-half inch of ice had formed during the night, 175 cocks were present; one hen appeared but stayed only a few minutes. On the morning of April 12, 355 cocks and 141 hens were present at one time. A few were observed mating. There were heavy clouds on the morning of April 13, and a fine snow began to fall soon after daylight. An 5:30, with a wind from the north and more than an inch of snow on the ground, 72 cocks and 3 hens were counted. As it snowed harder, the birds began to leave and at 5:55 a. m. the last two cocks walked rapidly away into the sagebrush. On the morning of April 20, there were approximately 350 cocks and 150 hens present. On April 21, a Golden Eagle flew by at 5:04 a. m., and nearly all the birds flew away but most of them soon returned, and a total of thirty matings was observed on this date.

For the next ten days the number of birds varied somewhat with the weather conditions, though there was a decided decrease in the number of hens near the end of April. On May 1, at 4:50 a. m., a count showed 302 cocks and 11 hens. On May 14, there were 174 cocks and 11 hens; on May 21, 238 cocks and 8 hens; and on May 24, 146 cocks and 5 hens. On June 13, two cocks appeared at daylight but left long before sunrise.

Briefly, then, the daily routine during the sexual cycle includes feeding and resting throughout the day, assembling in the late afternoon on the strutting grounds, leaving this area, as daylight fades, for roosting grounds near at hand or at some distance, returning at daybreak to the strutting grounds for the significant, main event of the day, and leaving singly or in groups before seven or eight o'clock for the more or less distant feeding and resting areas.

The daily activity during the mating cycle is, in general, as follows. The hens spend the day in nearby or remote areas feeding and resting. They may be accompanied by some of the cocks, but

usually the sexes are in separate groups. Cocks occasionally do some strutting during the day in the presence of hens. The cocks, as a rule, spend the major part of the day in feeding and resting in widely scattered areas, frequently two or three miles distant, and even farther away. Toward evening, the more virile and dominant cocks gather on the strutting grounds. The time of arrival depends, in part, upon present and recent weather conditions, but lags as the season advances. For example, on April 12 the first cocks arrived at 5:40 p. m.; on the 19th, at 6:27; on the 23rd, at 6:15; on May 3, at 6:50; on May 28, at 7:48. On the same dates, hens first appeared at 6:30 p. m., 7:00, 6:50, 7:30, and not at all, respectively. As soon as the cocks arrive, they take up their accustomed places, strut repeatedly, frequently challenge and occasionally fight a neighboring cock or one that is passing too near. By this sort of behavior, the virile cocks establish a degree of dominance on the area before the hens arrive. Increased strutting is very noticeable when hens are near or in sight. As darkness approaches, the birds leave singly or in groups, though a few cocks may remain until the last daylight fades. At the evening assembly, the number of cocks is only a fraction, never more than one-half, of those present at the morning concourse. It is harder to determine the number of hens present during the evening. I have never seen more than eleven hens in the evening at one time.

At night, some birds may roost in the immediate vicinity of the strutting grounds; others may be found at a distance of two or three miles or more. As the new moon gets higher in the western sky on succeeding days, the additional light influences some of the birds to remain on or near the strutting ground all night. This influence is most noticeable during the last eight or ten days before full moon. At such times, a large number of birds are present, including some hens. Strutting, challenging and fighting activities may occur at any hour of the night. Especially marked demonstrations, lasting an hour or more, have been noted beginning at 10:30 p. m., 11:45; 12:10 a. m., 2:00 and 3:30. At such times, hens have been seen wandering about the area, and the writer is of the opinion that an occasional mating may possibly occur at night, though none has been observed. The fact that no matings occur in the morning until broad daylight suggests, however, that this may not be true.

With the appearance of daylight, additional birds come in and a new demonstration begins that excels all others in magnitude and significant activities. In the number of cocks taking part, in the

volume of sound produced, and in the continuous activities of strutting, challenging and fighting, the maximum activity is reached shortly after daylight and before it is light enough to see a hen clearly at a distance of 100 feet. This is true whether the birds spend the night on the strutting ground or elsewhere. At this time, hens are coming into the area, and a little later, if a cock sees no hen near or approaching, he struts less frequently. However, a cock will continue to defend his station, and strut as a challenge to a rival or for the mere satisfaction of strutting. Occasionally he will stop to look around as if to observe the effect. At or near the mating spots, strutting continues with no respite until well toward the close of the morning assembly or until most of the hens have left the area. Later in the season, with few hens coming in, the cessation of activity becomes rather general after broad daylight, except at the mating spots and in the presence of hens that may be wandering through the area.

When all birds spend the night elsewhere, the first cock usually appears on the area at the first streak of dawn, and begins to *plop*. Within fifteen to twenty minutes, apparently all the cocks have assembled. The earliest morning hours at which cocks were noted appearing were: 3:45 on April 24; 3:45 on May 21; and 3:40 on May 29. As visibility becomes clear, the hens congregate on the mating spots, and the cocks remotely stationed strut less frequently; late in the season, such remote cocks may soon leave the area. However, a large number of cocks remain, and when the hens leave, after mating or after deciding they are not ready to mate, such isolated cocks put on a full demonstration of their strutting ability when hens pass near them. Occasionally, cocks near the outer edge of the area follow departing hens, strutting as they go. In such cases, we have never seen any mating, though the birds were carefully watched until well out of range. A considerable number of cocks always remain for some time after the hens have left the area.

In the morning dispersal, possibly more hens walk than fly away. As a rule, the cocks fly away in groups, occasionally accompanied by a few hens. Judging by the number of birds on the area, some of the cocks probably came from a distance of at least five miles. In dispersing, one group of cocks, observed two miles from the strutting ground, continued its flight for about one more mile.

ORGANIZATION OF THE MATING SPOTS

Dominance in the cocks plays a tremendously important role in the sexual life of this species, certainly not equalled in any other bird with which the writer is acquainted. On the area studied there were four well-defined mating spots, permanently located throughout the season, and each about the size of an ordinary room (pl. 15, fig. 2). At the height of the breeding season, two others were observed. At each of the principal mating spots the following individuals are to be found. (*a*) A compact group of hens occupying a space that is usually not more than 8 feet wide by 12 or 15 feet long. The number of hens present at first increases and then decreases as the season advances. (*b*) A master cock that parades back and forth, that struts near or among the hens and undertakes to do practically all matings. (*c*) The chief rival of the master cock, that is found strutting or standing near at hand and may be called the sub-cock (pl. 15, fig. 3). Under certain conditions, the sub-cock may take over a limited number of matings. (*d*) A group of guard cocks, usually three to six in number, that serve to keep away intruders which not infrequently attempt to ally themselves with these inner groups (pl. 15, fig. 1). The guard cocks are usually tolerated by the master cock and sub-cock, provided they do not come too close and mingle with the hens. They do a good deal of strutting but seldom do any mating.

In 1941, 174 matings were observed. In twenty cases, the dominance, or rank, of the cock was not determined. Of the remaining 154 matings, 114 (74%) were by master cocks, 20 (12.98%) by sub-cocks, 5 (3.24%) by guard cocks, and 15 (9.78%) by isolated cocks outside of regular mating spots or at hurriedly improvised ones. It should be added that the sub-cock mates only after the master cock has mated with many hens and there is an excessive number of hens ready for mating. The guard cocks have an opportunity to mate only late in the season and after the master cock and sub-cock are surfeited with repeated matings. After the peak of the season is over and near the close of the morning assembly, some hens that are ready for mating but have not been satisfied on the mating spots wander away and mate with cocks on locations outside of a regular mating spot. The conditions under which such matings occur will be described later.

The achievement of dominance by a master cock is not mere accident of location. As a rule the master cocks, sub-cocks and guard cocks are large and apparently older birds; size and weight

evidently are of some advantage. But the master cock is not always the largest cock in the group. He is the cock most ready to fight all comers, the most active, and apparently the most aggressive and vigorous bird. Such aggressiveness is probably determined as much by those internal secretions we call hormones as by age, strength and size. Dominance and winning of location are achieved by fighting, threatening, and bluffing and by the aggressiveness of the cock concerned. The cocks assemble on the strutting grounds once or twice daily some weeks before any hens appear and several weeks before any actual mating occurs. This period is characterized by strutting and those activities that establish dominance. Since the four principal mating spots had (in the present instance) the same general position on the strutting ground as in the preceding year, memory or some sort of conditioned reflex may have a part in determining dominance. The location chosen by an individual cock outside of the mating spots is usually a slight elevation with a level space on which the display of strutting can be easily observed from all directions. Frequently a cock on location has a rival that remains only a few feet away. Between these two, there is frequent scolding and bluffing and occasional fighting, but in general there appears to be watchful tolerance.

In making a threat or challenge, one cock charges or rapidly advances toward another and utters guttural, threatening sounds. If the challenge is accepted, a quick fight may ensue and, after a few blows, one cock may retire beaten. Otherwise the cocks 'square off,' side to side and head to tail, about fifteen to eighteen inches apart (pl. 15, fig. 4). Alert, with body, wings and tail quivering with excitement, both cocks take up the rapidly repeated, guttural challenge. Suddenly a wing lashes out, apparently aimed at the head of the opponent. If not surprised, the opponent may dodge or parry the blow and strike back in turn. A number of blows may be exchanged before they have had enough, and one bird slowly backs away (pl. 15, fig. 5). The victor proceeds to strut, and the vanquished may leave or continue to strut in his accustomed place. In the only instance observed where the beak was used, one cock was holding to the top of the head of another cock and giving him a vigorous, loud wing-beating. The unfortunate cock was trying to pull away, going headfirst. Ordinarily the vanquished cock retreats sidewise or runs away.

Strutting is primarily to express sexual urge and to attract the attention of hens. It may continue vicariously, either on a mating

spot or elsewhere, in the presence of a waiting hen or, early in the season, in the absence of any hen. Secondarily, strutting occasionally represents a challenge or the parade of the victor, and may arouse jealousy in another cock and lead to a challenge to combat. The vigorous master cock on a mating spot struts almost continuously, except when actually mating or repelling the advances of other cocks. Much the same is true for the sub-cocks. The guard cocks also do a great deal of strutting, except when engaged in driving off intruders. Throughout the area, all cocks strut almost continuously before it is light enough to see well and, after visibility, whenever hens are near or approaching. In a strut, the cock usually swallows air once or twice and then, with tail spread, head thrown back, and wings tense and partly extended, he advances three or four steps, making approximately a one-quarter or one-third turn, and further inflates the air sacs three times in quick, rhythmic succession. This is followed immediately by an audible, forced expulsion of the air, in which the breast is strongly contracted and the two large bare spots on the breast are rapidly reduced in size until they disappear. Following the audible expulsion of air (almost simultaneously) there is a resounding *plop* (fig. 11 of pl. 16 was taken only three-sixteenth of a second after fig. 9 of the same cock). The cock pauses for a moment to look around and observe the effect and then resumes strutting. A master cock may be so intent on strutting that he fails to observe, or even ignores, a nearby hen that is ready for mating. However, such behavior occurs usually after repeated matings with other hens and may be a sign of sexual satiety rather than lack of observation. In any case, there is no pause in strutting as long as hens are present.

The anatomical mechanism of strutting has not been completely worked out; the following will serve only as a general description. The lateral walls of the esophagus in the cocks are very highly elastic and the air sacs are simply great expansions of this portion of it. The air sacs reach their maximum development during the regular strutting season and are reduced in size at other seasons. The esophagus is muscular as well as elastic, and certain muscles that have their origin on the body framework are inserted on it. The skin over the breast region is highly elastic and muscular. A series of muscles also connects portions of the skin in this region with the body structure. Slow-motion moving pictures indicate that the process of pumping air into the esophageal air sacs involves three forced inhalations and exhalations in rapid succession. It

appears that each inhalation quickly fills the lungs and the air sacs connected with them. This accumulated air is forcibly expelled into the esophagus, during which process the nostrils are undoubtedly closed. During the succeeding inhalation, the opening into the esophagus is apparently at least partially closed, and the air sacs drop to a lower position. After the third inhalation is forced into the air sacs, the air is allowed to escape and, when the wings are raised, there is a strong contraction of muscles affecting the median line of the mechanism and the areas surrounding the bare spots. This results in the rapid contraction or 'swallowing' of the two bare areas on the breast, and their complete disappearance is accompanied by a resounding *plop* (pl. 16, fig. 11).

The head may disappear at the maximum stage of the strut (fig. 12). Note the same bird five-eighths of a second later, after the conclusion of the strut (fig. 13), as a pause is made to inspect the effect. While the air is being forced into the esophagus the wings are down and pressed close as in fig. 8. During an inhalation the wings are raised and partly spread as in fig. 10, taken one-half of a second after fig. 8. Note also the rapid change of position of the air sacs. This up-and-down movement of the air-sac mechanism, followed by the sudden collapse of the air sacs gives a fantastic, grotesque appearance to the strut.

On a still morning the *plop* can be heard for a half mile or more. The quick inhalations may sometimes be heard at a distance of twenty to thirty feet. Early in the season, the third exhalation is usually vocalized, expressed as a whistle-like *purp*. Later in the season, it may be only a sort of soft, whistled *wherch*. After the *plop,* partial deflation takes place automatically, without sound, as the result of the elastic reaction of the involved tissues, which are very much stretched in inflation. Frequently, in deflating, there is a guttural belching sound, and a cock may partially deflate by spasmodic contraction of muscles along the median line, thus exerting pressure on the air pouches. Cocks have been seen to deflate by opening the mouth and stretching the neck, without making any sound.

BEHAVIOR OF HENS

The hens did not appear on the strutting ground in March until two or three weeks after strutting began. They gradually increased in numbers, but no mating was observed until the second week in April. Of 174 matings observed in 1941, 142 occurred from April 20 to April 26, inclusive. It was, of course, impossible to observe

Figure 1

Figure 2

Figure 3

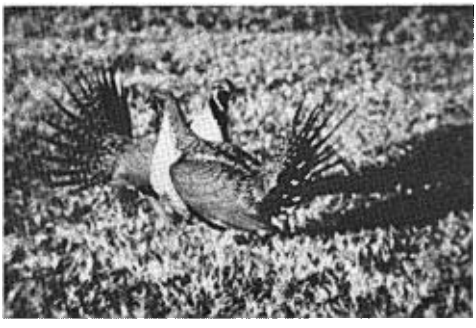

Figure 4

Figure 5

MATING BEHAVIOR OF THE SAGE GROUSE.

all matings. Though a hen may appear on the strutting ground several mornings in succession before mating, one successful sexual union appears to be all that is needed. We have observed a hen mate more than once, but usually late in the season and after a mating of doubtful success. After a successful mating, hens probably do not return to the area. Even during the height of the season, we believe that considerably fewer than half of the hens appearing on any one morning are successfully mated. On the morning of April 12, we saw six matings, when 141 hens and 355 cocks were counted. It was estimated that not more than ten other matings occurred on this date. On May 21, four matings were observed, when 238 cocks and 8 hens were counted. Three matings occurred on May 29, when 146 cocks and 5 hens were present. The breeding season therefore spreads over at least forty-seven days. The cocks appear some four or five weeks before any matings occur, and return for ten days or more after the last matings.

Weather conditions remaining the same, the number of hens at the evening assembly, except late in the season, is rarely ten per cent of those that appear the next morning. The hens appear at the evening assembly fifteen to forty minutes later than the cocks, and leave when the cocks do. At the morning assembly, the hens appear from ten to thirty minutes after the cocks arrive, and leave soon after mating, always in advance of the cocks.

Many hens walk into the strutting ground. Others fly in, but seldom alight in the central part of the area. If ready to mate, they may walk with little hesitation almost directly to a mating spot. Generally, as they walk into the area, they appear to be quite indifferent to the grand demonstration that is put on in their presence. They wander about the area and pause here and there to pick up food; they stop to rest or to look around; sometimes they stop near a cock that seems impressive, but usually go on after a while and show very little interest in the whole proceeding. Such hens may or may not join other hens on a mating spot, depending upon how nearly they are ready for mating. If not ready for mating, they linger for a while, then leave the area to return the next morning.

In general, the behavior of hens on the strutting grounds is inconspicuous and passive (pl. 15, figs. 2, 3). On the mating spots, the hens exhibit a mild sort of 'peck dominance' when in competition for the attention of the master cock. This is especially noticeable when a considerable number of hens are ready for mating. One hen may then drive other hens away from near the master cock.

On one occasion, a hen in an apparent fit of disappointment and jealousy took one vicious peck at a cock, which was not resented. At the height of the mating season, it is not unusual to see fifty to seventy hens standing around in a rather compact group. Early in the season they are more scattered. There is no fighting, and they appear rather unconcerned; 'peck dominance' is seldom seen. Occasionally a hen may preen her feathers or sit down and rest while patiently waiting. If a cock approaches too closely, as if to mate, the hen steps quickly to one side or runs away a few feet. A hen nearly ready to mate shows more interest, and approaches nearer to the path of the strutting master cock; but some time may elapse before she signifies to the cock her readiness for mating (pl. 17, fig. 14).

The behavior of hens on the strutting grounds has been described in different portions of this paper. Briefly summarized, the hens gather in the area later than the cocks, but frequently a day or more before they are actually ready for mating. They wander about the area, apparently little concerned, but actually inspecting the cocks and looking for the location of a mating spot where other hens are present. Here they quietly await their turn, and if not quite ready for mating, soon wander out of the area to return at a later date. If their invitation to mating is accepted by the master cock, they soon afterward leave the area, probably not to return until the following year. If competition is keen for the attention of the master cock, the hens make a querulous *quer, quer, quer,* as if complaining or begging, and one hen may peck at another and drive her away from near the master cock. At the height of the season, if attention from the master cock is not forthcoming, one hen may mount another and even go through the entire act of mating. We have seen as many as four hens in a heap trying pseudo-mating (pl. 17, fig. 17). When a hen comes into the area late in the season and the chief mating spots are no longer continuously occupied, she wanders about as if uncertain what to do, tarries at intervals, apparently looks over several cocks, and may mate with an outside cock or leave the area without mating. In one instance we saw a hen, eight minutes after mating with the master cock, indicate to a second cock twenty feet away that she was ready for mating; two minutes later she left the second cock without mating, went past the master cock to tarry near a third cock sixty feet farther on, and then went on past a fourth cock and out of the area.

BEHAVIOR DIRECTLY RELATED TO MATING

Simon has given a good description of the behavior of cock and hen preliminary to coition. The hen signifies readiness for mating by squatting in front of the cock with outspread wings usually touching the ground (pl. 17, fig. 14). Frequently the wings are fluttered to attract attention. The cock starts forward as if to strut but, instead, steps up on the back of the hen and ordinarily, with head held high, braces himself with his downward extended wings. He quickly brings his tail down, brushing aside the tail of the hen, presses his outspread tail firmly against the ground, thus tilting the body of the female forward, and within a few seconds completes the act of coition (figs. 15, 16). Sometimes the cock remains standing on the back of the hen for two or three seconds after coition is complete. He then slides or steps off and resumes strutting. The hen gets up quickly, runs a short distance and vigorously shakes out and ruffles her feathers. After shaking herself repeatedly, she usually spends some time preening and then marches, or occasionally flies, off the strutting ground, apparently taking no further interest in the area. If the master cock is exhausted by too many or too frequent matings, he may ignore an invitation to mate and go on strutting, or may step up and stand on a hen without making any attempt at coition. At times the hen is covered completely at the sides and rear by the wings and tail of the cock, and in front by the pendulous folds of his breast. On two occasions we have seen a cock seize and hold the top of the head of a hen, as is the manner in domestic chickens. If a hen is approached by a cock when she is not ready for mating, she steps briskly to one side or runs a few steps forward.

The time of day at which mating occurs is interesting and probably is a helpful adaptation for protection against the most dreaded of all enemies, the Golden Eagle. Golden Eagles seldom fly over the strutting grounds before sunrise. Our records indicate that more than fifty per cent of all matings occur before sunrise. On April 21, at 7:40 p. m., just before dark, the movements of a cock observed with 6-power glasses indicated that he was mating with a hen, though the hen could not be seen. On May 20, at 6:17 p. m., a hen was seen to shake out her feathers vigorously, preen herself, and soon walk away, acting as if she had just mated. We have not seen any matings at night. However, such matings occasionally may occur under the influence of the full moon, at the height of the breeding season, but certainly they do not occur often. The presence of a

large number of strutting cocks and some hens wandering about the area, sometimes in small clusters surrounded by cocks, offers circumstantial evidence for this possibility. In the morning, mating does not begin until visibility is clear at one hundred feet or more. Perhaps lack of a minimum amount of light is a factor inhibiting night mating. Mating began on April 20 at 5:20 a. m.; April 21, at 4:42; April 22, at 4:43; April 24, at 4:35. Once started, mating goes on rather rapidly for a time unless disturbances occur.

We have noted that the birds return to the same strutting ground year after year. Barring accidental changes in the environment, like snowdrifts, the mating spots in the area studied in 1941 were approximately the same as those used in 1940. On this large area we have seen only five mating spots in use at one time. The size of such a spot depends upon the number of hens. A mating spot, accommodating sixty-five hens at the height of the season, was approximately ten by fifteen feet. The guard cocks were a few feet outside this area. Sometimes early in the season the hens are more scattered (pl. 15, fig. 1) but mating usually occurs only near the central spot. A snowdrift temporarily dislocated one of these spots. The new location infringed on the territory of adjacent cocks. Some seventy hens gathered on the new location early one morning, but there was so much commotion and fighting that the master cock had great difficulty in repelling encroaching cocks, and had little time for mating. The hens soon began to leave for an adjacent well-established spot about one hundred feet away where there was little fighting, where mating was frequent, and the supremacy of the master cock was not disputed. Within thirty minutes nearly all the hens had deserted the disorderly mating spot.

The social organization of a typical mating spot is fairly well defined, and may be summarized as follows: At the center is a group of hens which, if not immediately ready for mating, stand around quietly in a rather compact group. If a hen starts to leave the group, she is not molested, though some cock may perform a few struts for her particular benefit. If a hen is ready for mating, she usually manages to get near the strutting master cock that dominates the whole group. There are also present the sub-cock, or chief rival of the master cock, and several guard cocks, or cocks-in-waiting, that are subordinate to the other two. Occasionally an outside cock attempts to break into this group; usually he is driven off but, if persistent, he is tolerated a short distance away and so may be added to the list of guard cocks.

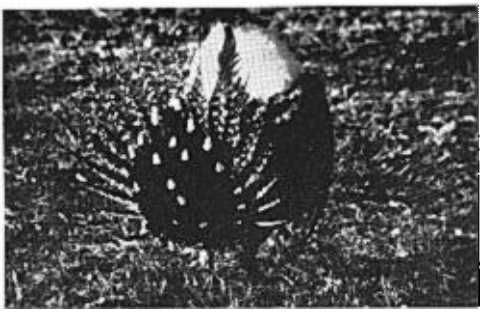

Figure 6

Figure 7

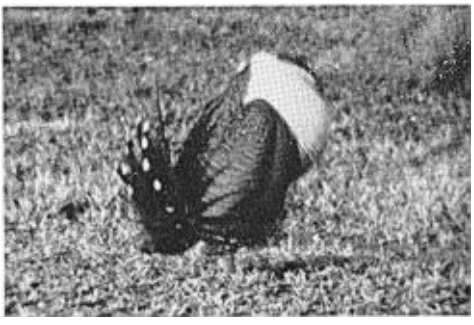

Figure 8

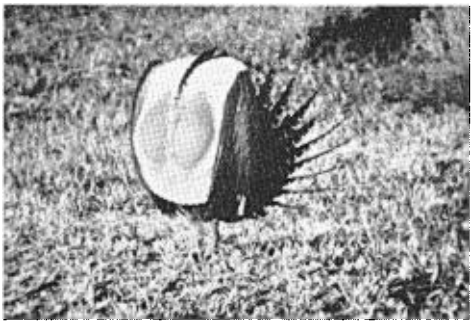

Figure 9

Figure 10

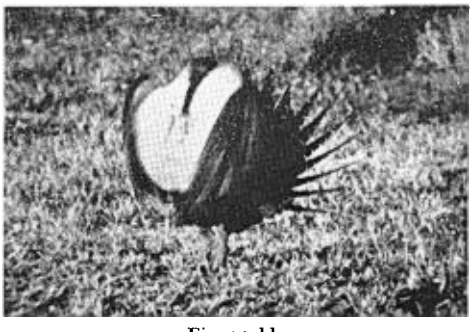

Figure 11

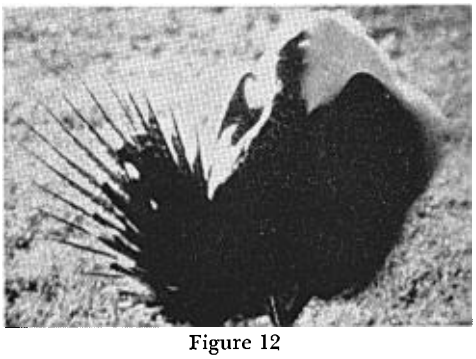

Figure 12

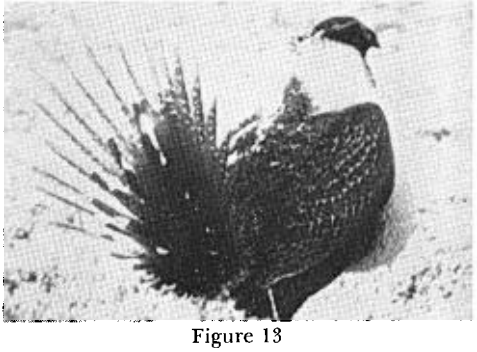

Figure 13

MATING BEHAVIOR OF THE SAGE GROUSE.

The functions of the master cock are: strutting, which appears to be done chiefly for his own satisfaction and for the benefit of the females; fighting and threatening, for the purpose of keeping general control of the other cocks; and, of supreme importance, mating with the hens. The cock, after mating, usually looks around (pl. 16, fig. 13), and if he suspects no intruder, soon begins to strut again. If he discovers a rival (sub-cock or guard cock) near some of the hens, he makes a threatening charge, and if the rival does not give ground, a fight may ensue. Occasionally a cock may become incensed at the sight of another cock in the act of mating and charge fiercely at the mating cock. Sometimes a mating is broken up in this way. On April 20, it was noted that occasionally, when the master cock was busy mating or chasing some other cock away, the sub-cock or a guard cock might mate with a hen near him. Late in the season, the master cock may continue to strut, apparently entirely ignore an invitation to mate, and at the same time fight off other cocks to prevent their mating. On May 21, at 6:46 a. m., a hen signified that she was ready to mate but she was not accepted by the master cock. Again at 6:49 and at 6:51, she was anxious to mate but was again ignored. At 7:00, the hen walked over near the sub-cock and signified readiness to mate, but the master cock attacked the sub-cock and prevented mating. At 7:05 the master cock attempted to mate with this hen, which was then between the two cocks, but he was fought off by the sub-cock. At 7:10, the same attempt was made with the same result. Soon after this, the hen left the area.

The number of matings of which a master cock is capable in a single morning is not known. On April 21, a master cock on one spot mated with four hens before all the birds were frightened away by a Golden Eagle. After the birds returned, the master cock on the same spot mated with eighteen hens. Probably both series of matings were by the same master cock. On April 22, a master cock mated with twenty-one hens. On April 24, a master cock mated with fifteen hens. Mating begins early in the morning, and, once begun, usually proceeds as rapidly as capacity and other duties of the master cock permit. On April 21, a master cock mated five hens in nine minutes (4:42–4:51 a. m.), another mated four hens in five minutes (4:55–5:00 a. m.). On April 22, a master cock mated the first six hens in seven minutes, and the first nine hens in thirteen minutes. Later in the morning and later in the season, mating proceeds more slowly even though many hens are ready to mate.

On April 24, we observed eighteen matings before sunrise, and nineteen matings after it. The earliest mating observed was on April 24 at 4:35 a. m., fifty-two minutes before the rays of the sun fell on the area.

Evidence of sexual satiety or temporary incapacity is indicated by the following observations. One of the cocks mentioned, on April 22, at his eighth mating (in twelve minutes), held his head high and remained on the hen a long time; after the act was completed the hen did not shake herself as is customary after a definitely successful mating. This same master cock, after the thirteenth mating, mounted another hen but did not succeed in mating, apparently due to temporary incapacity. Three minutes later he made another abortive attempt to mate but, on seeing a second hen mount a third one, he immediately deserted the first hen and mounted the second one which slid off the third. He took some time to mate and, while so doing, was attacked by another cock. On April 26, abortive attempts at mating were very frequent after the master cock had made a few matings. On May 11, as early as 4:20 a. m., a master cock paid no attention to a hen that was ready to mate but, instead, fought with a guard cock.

The sub-cock usually accepts the dominance of the master cock. On April 22, a sub-cock mated with his first hen after the master cock had mated with fifteen, and mated with a total of four hens as compared with twenty-one by the master cock. On April 21, a sub-cock mated with a hen on the edge of a group and was attacked by the master cock which up to that time had mated only twice; later the sub-cock attacked the master cock while mating with the thirteenth hen. On April 24, a sub-cock made his first mating after the master cock had mated ten hens. After twelve matings by the master cock, the sub-cock attempted to mate again but was attacked by the master cock. On one spot, on April 26, there were ten matings by the master cock, eight by the sub-cock, and five by guard cocks, the matter of dominance being gradually taken over in the order given. On May 11, as the master cock started his first mating he was attacked by the sub-cock; a few minutes later, after the latter mated, he was attacked by the master cock. This will give some idea of the relative position of the chief rival of the master cock.

The rôle of the guard cocks has been mentioned. They help to keep intruders away from the groups of hens and, as long as they keep a proper distance from the hens, are tolerated by the master cock and the sub-cock. They also tend to take over the mating

when vigilance slackens or when the master cock and sub-cocks are surfeited with mating. On April 26, after the master cock had mated with six hens and the sub-cock with seven, a guard cock attempted his first mating with another hen but was driven away by the master cock. Shortly after this a guard cock mated, but was attacked by the master cock. Later, after the master cock had mated with the eighth hen, a guard cock made a third and fourth mating. Still later when a guard cock started to mate, and again when he mated, he was attacked by both the master cock and the sub-cock. Still later in the morning, when a hen indicated to a guard cock that she was ready to mate, the guard cock was attacked by the master cock.

Under certain circumstances, improvised mating spots may be organized. One morning an eagle frightened all the birds away. After about thirty minutes, when they were coming back, a cock, stationed near the edge of the area, succeeded in stopping five or six hens at his location. He mated with one of these before the others wandered on into the central area. Another improvised mating spot was observed the same morning under similar circumstances, but here dominance among the adjacent cocks had not been firmly established; there was much fighting and commotion and the hens moved on into the central area after one of the hens had mated with an adjacent cock. Late in the season, when hens are not receiving attention on a regular spot, they may wander away to a new, improvised mating spot established by some outside cock. This has been observed three times.

The cocks stationed all over the area outside of regular mating spots spend their time defending their own particular territories and trying to attract the attention of hens coming into or leaving the area. Except for one morning when the birds were returning after being frightened away, as mentioned above, none of these cocks, so far as our observation went, succeeded in mating with hens as they were coming into the area. Usually outside cocks mate only with hens that have not succeeded in being mated on the regular mating spots and as they leave the area. They may or may not pass several outside cocks before mating. On April 24, at 7:57 a. m., the last hen walked away from a mating spot and mated with a cock fifty feet away. On May 9, at 5:10 a. m., a hen indicated to the master cock she was ready to mate, but she was ignored. Five minutes later she left, stopped to linger near two cocks fifty feet farther north, and at 5:16 went on, passed another cock at 5:17, turned

southwest, and at 5:19 mated with another cock one hundred feet from the last. The outside cocks have a subordinate but important place in the social order. Plate 17, figure 20 shows a cock ready to leave the strutting ground, after the morning assembly.

HETEROCLITES

Two to three per cent of the male birds may be termed heteroclite cocks. These heteroclites have about the size but not the full feathering of normal cocks. The form of the body is somewhat between the two sexes. They do not strut and will not fight with other cocks, and they are particularly detested by full-plumaged cocks. When one passes through the area, each stationed cock in turn chases him with such energy that the heteroclite frequently takes to flight. Occasionally one manages to sneak into a group of hens on a mating spot and as he dodges around among the hens, the master cock, sub-cocks and guard cocks frequently have some difficulty in driving him away. On one occasion, we saw one start to mate with a hen, but he was driven away by the master cock. In general, these birds behave more like hens than cocks. Their hormone system is evidently out of adjustment. No attempt has been made to study their anatomy.

From two to three per cent of the female birds may be termed heteroclite hens. These are slightly larger in size than other hens, with the tail somewhat longer than that of the average hen, and the bare spots on the breast are much smaller than those on the cocks but a little larger than those on average hens. On the mating spots they have a decided peck dominance and are frequently active in keeping other hens away from the master cock. At times they will spread the tail and go through all the motions of a complete strut (pl. 17, figs. 18, 19). They are not able to *plop,* due to the relatively small size of the air-sac expansions of the esophagus and the size of the bare spots. At the height of the mating season, when numerous hens are ready for mating, we have seen such a heteroclite hen go through with the complete mating process with another hen; a little later she was mated twice by the master cock. When a heteroclite hen is mated, she is usually not satisfied with one mating but continues to exhibit sexual behavior. Evidently the hormone system of these birds also is out of normal adjustment.

ANOMALOUS BEHAVIOR

This peculiar polygamous system of the Sage Grouse has been remarkably successful in times past when this bird ranged in enor-

mous numbers over an area equal to about one-third of the United States. However useful it may have been in perpetuating the species, the system breaks down at the height of the breeding season when many hens on a mating spot are ready for mating. We have seen three and four hens piled in a heap trying to mate with each other while the temporary incapacity of the dominant cock and the restraint of the system on the other cocks prevented these hens from being mated. As the morning sun rises higher in the sky, the instinct to leave the area transcends all others, and some of these hens fly away unsatisfied. Others may walk through the area and fall temporarily under the spell of an outside cock whereupon nature's chief act is accomplished. In this way the weakness of the system is, in part, compensated.

The pseudo-mating of one hen with another may result in apparent satisfaction to one or both. A master cock was noted looking on while one hen mounted another, but he did nothing. Later the same morning, this master cock again watched a hen mate with another and did nothing. He probably would not have allowed another cock to do this.

The heteroclites of both sexes, as previously described, present other types of anomalous behavior. While their behavior may possibly be explained as hormonal or hermaphroditic irregularities or changing sex in some older hens, there are some phases of their conduct that are peculiarly confusing. We have seen a heteroclite hen engage in the following sequence of acts: mate in the role of a cock with another hen, chase other hens around, strut like a cock, be mated by the master cock, mate with a hen, be mated by the master cock, and mate with a hen,—all within two hours and twenty-one minutes. What the significance of such behavior may be we will not attempt to answer. Such hedonistic behavior does not appear to come within the pale of the system. The following is another example. One morning late in the season of 1940, not twenty-five feet from a regular mating spot, we saw the same cock mount the same hen twenty-two times in the space of one hour. Copulation, or attempted copulation, took place only on the third, fourth, seventh, eleventh, fourteenth, seventeenth, eighteenth and twenty-second starts. This cock was attacked only once by his chief rival that stood near by, though the whole procedure evidently came under the observation of no less than six or eight cocks. Probably no actual copulation took place, for the hen did not act as if mated and so far as we noted her tail was not raised.

Even more abnormal behavior is sometimes shown by cocks. In a few instances we have seen an outside cock mount a dunghill, squat, and go through most of the movements characteristic of actual mating.

UNSOLVED PROBLEMS

This paper has opened up a new chapter in Sage Grouse study and has left many unsolved problems. Does the same cock occupy the same location on successive mornings? We believe that he does, except as he may advance by challenge and contest to a more favorable one; in the new location he probably becomes the tolerated, chief rival. Seldom have we seen a cock driven from an established location, and we have not followed the resulting behavior. Does the same master cock preside over the same mating spot in successive assemblies? Again we believe this is true for the following reasons; we have no direct proof.

(1) On each mating spot there is, as a rule, a rather regular routine; that is, there is a well recognized dominance evident on the same mating spot morning after morning. When dominance is disturbed, confusion and chaotic conditions tend to develop. (2) During the mating season, several large cocks were killed by flying against a barbed-wire fence which separated two portions of the strutting ground, others by eagles, and possibly one or two by coyotes. One morning after a large cock had been killed on the barbed wire, it was noticed that dominance was uncertain on one of the mating spots; previously the behavior on the spot had proceeded in the ordinary fashion. Finally one of the cocks present dominated the area. (3) After a snowstorm, a snowdrift displaced by twenty to thirty feet one of the well established mating spots. This threw the group of cocks in that area out of relative position, for they do not strut on the snow. A large group of fifty to sixty hens collected near the snowbank, but there was so much confusion and the master cock had so much trouble with other cocks that he had little time for strutting or mating. There was also fighting among other cocks. After some time, the hens began to leave and go to another mating spot about forty yards away where dominance was well established and mating was proceeding in regular order.

I have the opinion that shortly after the peak of the season, the master cock, surfeited with much mating, may not return to the area, and that in his absence the sub-cock takes over dominance on the spot. However, there is no direct evidence for this belief. Further work is needed along these lines, as well as to explain the nature of the heteroclites and other anomalous behavior.

We are of the opinion that ordinarily a hen requires only one mating annually. This is indicated by the fact that after an evident successful mating, the hen leaves the mating spot, appears well satisfied, displays no more interest in the area, and soon leaves the strutting ground (pl. 17, fig. 21). Indirect supporting evidence is furnished by the following. Let us assume that the number of hens using this strutting ground equalled the number of cocks (about 400). When we take the number of matings observed each morning and the number of hens present, and allow similar ratios for those dates when no observations were made, the result indicates there were approximately 400 matings on this strutting ground during the season.

After mating, the hens lay no eggs for two or three weeks, and sites selected for nests are very widely scattered. On the contrary, cocks are ordinarily found in groups, usually miles away from the strutting areas. Girard has made some study of the Sage Grouse in summer. Bond (1900), Forbush (1917), Horsfall (1932), Girard (1937), Bailey and Niedrach (1939), and Simon (1940) have added much to our knowledge of the habits of the Sage Grouse. (See Simon, Auk, 57: 471, 1940 for references.) If we are to preserve this fine western game bird, an intensive study of the ecological relationships involved throughout the year is urgently needed.

SUMMARY

The mating habits of the Sage Grouse have been studied for two seasons and for one entire mating cycle lasting from early in March to near the middle of June. The strutting ground studied, about one-half mile long and 300 yards wide, accommodated 400 cocks and an estimated equal number of hens. An extraordinary system of polygamy prevailed in which dominance in males was based on fighting, bluffing, and strutting display. Practically all mating took place on five mating spots, each not much larger than an ordinary room. Each spot was occupied by: a more or less compact group of hens; a dominant, master cock that did most of the mating; his chief rival or sub-cock that took over some matings under certain conditions; and several guard cocks surrounding the group of hens that aided in keeping intruders away, and rarely were allowed to mate with hens. The remaining cocks were on widely distributed locations, singly or in pairs. Of 174 observed matings, dominance of cocks was observed in 154. Of this number, 114 (74%) were by master cocks, 20 (13%) by sub-cocks, 5 by guard cocks, and 15 by outside cocks under conditions where the system tended to break

down. Mating took place only upon invitation of the hen. Only the most aggressive, most vigorous, and usually the larger cocks attained the rank of master cock. Both cock and hen heteroclites were observed. Certain types of abnormal sex behavior were noted. Other behavior and correlated habits are briefly described.

EXPLANATION OF FIGURES

Plate 15, fig. 1. Loosely dispersed mating group early in the season. Hens, master cock (R. Center), sub-cock (L. Center), three guard cocks, other scattered cocks.
2. Master cock and twenty-two hens.
3. Master cock strutting; sub-cock and thirteen hens.
4. Cocks in fighting position.
5. Cocks fighting.

Plate 16, fig. 6. Cock strutting, rear view.
7. Cock strutting, side view.
8. Forcing air into esophagus; wings low and close to body.
9. Maximum inflation.
10. Drawing air into lungs and air spaces, one-half second after fig. 8. Compare altered position of wings and air sac.
11. Deflation (just after *plop*); three-sixteenths of a second after fig. 9. Note disappearance of bare spots.
12. Head of cock may disappear at maximum phase of strut.
13. Five-eighths of a second after fig. 12. Cock pauses to look around.

Plate 17, fig. 14. Hen signifies readiness for mating and is accepted by the master cock; sub-cock nearby.
15. Mating, side view. Head of hen may be seen.
16. Mating, front view.
17. Two hens mounting a third.
18. Heteroclite hen strutting.
19. Heteroclite hen, strutting. Compare size with master cock and other hens.
20. Cock resting after hens have left; about ready to leave.
21. Hen ready to leave strutting ground.

University of Wyoming
Laramie, Wyoming

Figure 14

Figure 15

Figure 16

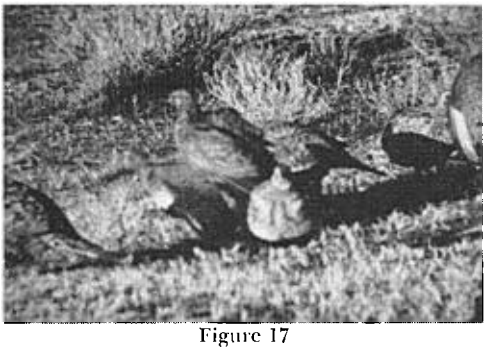

Figure 17

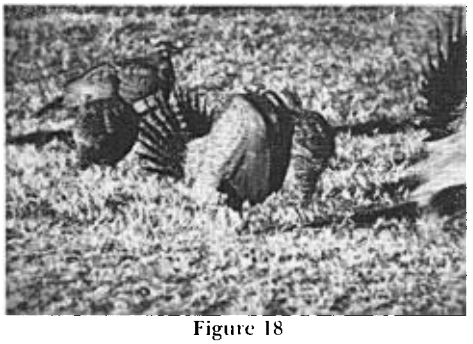

Figure 18

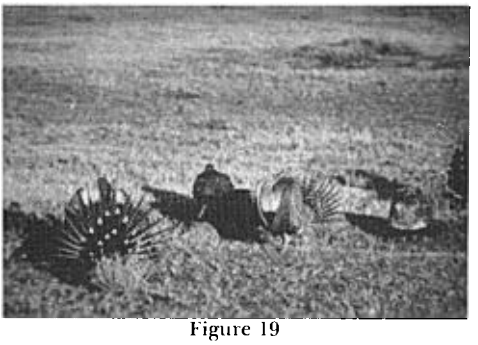

Figure 19

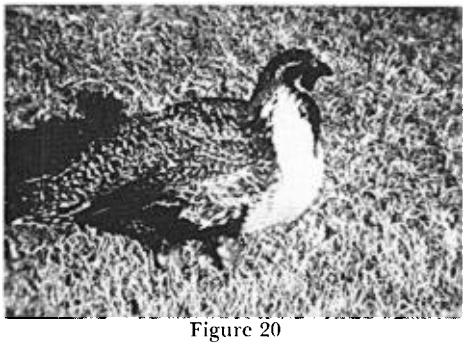

Figure 20

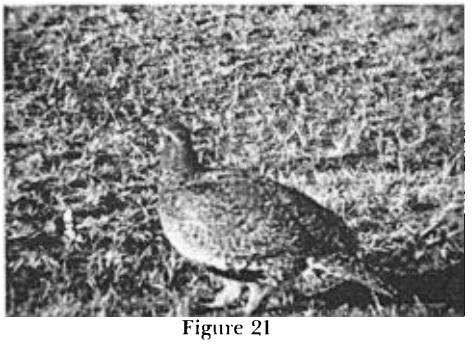

Figure 21

MATING BEHAVIOR OF THE SAGE GROUSE.