MOVEMENTS OF FEMALE RUFFED GROUSE DURING THE MATING SEASON[1]

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KNOWLEDGE of sexual relationships in the Ruffed Grouse (*Bonasa umbellus*) is inchoate. Displays related to mating have been described (Allen, 1934; Bump et al., 1947), but two basic questions remain unanswered in the literature. Is the hen attracted to the site of the cock's drumming performance, and do the cock and hen form a pair-bond that is more than transitory?

Hens, and cocks to a lesser degree, are seldom observed because of their cryptic behavior within dense vegetation. For this reason, reports on mating behavior have been deductions supported either by general observation in the field or by extrapolation of observations on captive birds.

Bent (1932, p. 146) did not comment on pair-bonding, but he did speculate that the cock leaves its drumming log and seeks out the hen. Roberts (1932, p. 380) apparently favored the "opinion" that the Ruffed Grouse is polygynous. Leopold (1933, p. 104) considered the mating behavior to be similar to that of the Ring-necked Pheasant (*Phasianus colchicus*), in which each male has its own separate group of hens. Grange (1948, p. 192) did not know whether Ruffed Grouse pair or are polygamous, but he "guessed" that they pair for the season, while Edminster (1954, p. 231) stated that the Ruffed Grouse is promiscuous in its breeding habits. Lack (1940) developed a classification for pair-formation in birds and placed the Ruffed Grouse among those species in which the sexes meet solely for copulation and in which the female goes to the solitary male at its display site.

Allen (op. cit.), after 15 years of study of captive Ruffed Grouse, presented evidence which allows interpretation of the duration of the pair-bond. To complete the sequence of events described by Allen—synchronization of mating cycles, dominance, copulation—would require, it seems to me, at least a few days. Pair-bonding would not be a transitory affair and polygyny is indicated.

Bump et al. (op. cit.), after a long-term study of captive birds, observed the reactions on which Allen's conclusions were based. They did not believe that a synchronizational period is necessary to ensure fertilization of eggs. It seemed probable to them that the female in the wild would seek out the male in his territory; if they were both in the proper stage, copulation would take place; if not, the hen would retire to return later or to move on to another drumming male. Because of a postulated evenness of the sex ratio

[1] Paper No. 5842, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul, Minnesota 55101.

and the dispersed nature of the mating birds, the likelihood of a hen moving on to another male would be slight, and this, they reason, would be tantamount to "enforced monogamy."

These observations and studies have yielded valuable information but as Lack noted many years ago (1940), studies on the mating behavior of captive Ruffed Grouse do not necessarily apply to wild birds. However, only recently (see Marshall and Kupa, 1963) was the technique of radio-telemetry adapted for use on Ruffed Grouse and thereby made possible the study of that bird's behavior under field conditions. I have used the telemetric method to obtain data on the basic question of pair-bonding in Ruffed Grouse. These are, I believe, the first field data on this behavior.

This study was done during the spring of 1963 at the Cloquet Forest Research Center, University of Minnesota. Gullion et al. (1962) have described briefly the soils, topography, and vegetation of the Station. In general, peat soils supporting black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), and larch (*Larix laricina*) are found in the lowlands; the aspens (*Populus spp.*), white birch (*Betula papyrifera*), white spruce (*Picea glauca*), and jack and red pines (*Pinus banksiana* and *P. resinosa*) predominate on the loamy-sand uplands.

METHODS

Because cocks seldom left their drumming-activity centers (the immediate area around a drumming log according to Gullion et al., 1962), the problem of pair-bonding was best attacked through a study of the movements of hens. Radio-tracking was initiated in February so that home range boundaries were well defined before the breeding season began. I succeeded in radio-tracking three hens (all immatures) through their mating activities and onto their nests. An additional hen (an adult) was tracked but I failed to find her nest.

The birds were taken in "lily-pad" traps and leg bands were affixed as detailed by Gullion (1965). A radio-transmitter package modified from that of Marshall and Kupa (1963) as described by Brander (1965) was then attached. Both the performance of the female birds in flight and their participation in social behavior indicated that the movements to be described are not significantly different from those of unmarked birds.

As a rule, three precise locations were determined daily for each bird. Precision was of an order which allowed placement of a bird within a quadrat 33 feet square (0.025 acres). Locations were taken at mid-morning, mid-afternoon, and during the night-roost period. Transmitter signals were also monitored several times during the day so that the general location of a bird was under rather constant surveillance.

The locations of all drumming-activity centers were also known. At least

TABLE 1
CALCULATED DATES OF FIRST EGG AND OESTRUS FOR THREE HENS

Bird number	Date on nest	Number eggs	First egg	Oestrus
1826	23 May	9	9 May	3– 6 May
1944	19 May	6	11 May	5– 8 May
1828	24 May	8	13 May	7–10 May

two cocks within the study area were associated with drumming-activity centers but did not engage regularly in drumming performances.

For purposes of evaluation, I used information in the literature to calculate the probable dates on which certain responses by the hens might occur. On the average, Ruffed Grouse lay two eggs each three days until the clutch of 9 to 14 eggs is complete (Bump et al., 1947). Knowing the number of eggs laid by a certain date, one may derive the date of first egg. Bump et al. (op. cit.) also determined that captive hens were in oestrus three to seven days prior to the laying of the first egg, the shorter period being more frequent. The onset of oestrus was abrupt and if the hen were mated promptly, oestrus ceased almost at once, but otherwise it lasted for three to five days. [Oestrus is a term usually reserved for the class Mammalia (Bullough, 1961) but Allen (1934) and Bump et al. (1947) apply it to the Ruffed Grouse and I follow their usage.]

Using this information, I calculated the date of first egg for the three hens and the dates that each hen might have been in oestrus. The results are presented in Table 1.

Location and movement maps for the theoretical oestrous period were constructed. These maps and interpretations are now considered for each bird in turn.

RESULTS

Hen No. 1826.—The movement pattern of this bird from the morning of 1 May to the morning of 10 May is given in Figure 1. Actually, the mating season for this hen was adumbrated by her response to drumming activity, first on 25 April then on 27 and 28 April. On each of these dates she moved a short distance in the direction of a drumming-activity center but returned to her established winter range, a well defined area of 26 acres. The drumming of DR1 (Fig. 1) and another male in that area were, apparently, the stimuli involved. Nothing more than movement response was indicated.

Then, on 1 May, she made a long northerly movement toward an activity center but returned to her winter range that same evening. She did not approach the drummer (DR2) which, probably, elicited her movement response. On 3 May she again made a move to the north, and this time approached the drumming log of DR2. After spending the night in a larch stand 500 feet west of his log, she returned to her winter range. This was followed the next day (5 May) by a shorter northerly probe and retreat. The next move, on 6 May, was unalterably to the north. Supposedly, 6 May was the

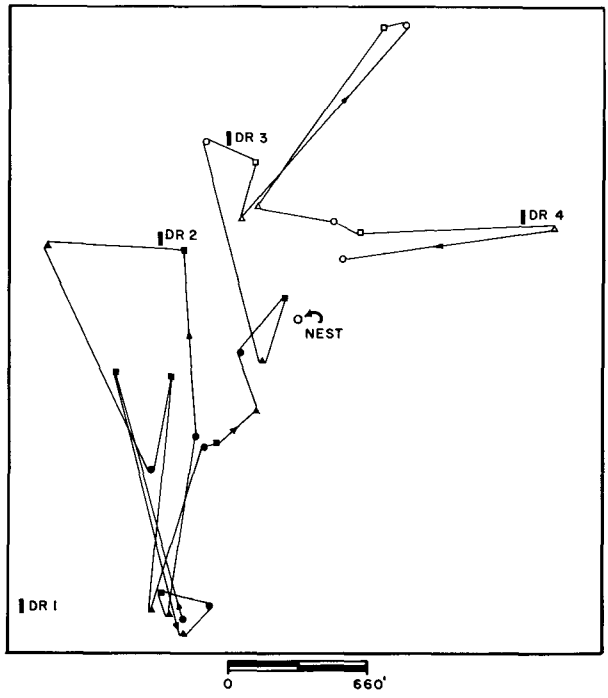

FIG. 1. Immature female, No. 1826. Movements and locations during oestrus, 1–11 May. The 1 May location is in the southwestern part of the figure. DR and black rectangle indicates a drumming male. Circles, squares, and triangles represent mid-morning, mid-afternoon, and night-roost locations respectively.

last day of oestrus (Table 1). Open symbols are employed in Figure 1 for locations thereafter (7, 8, 9, and 10 May).

She had already visited the activity center of one drummer (DR2) and then began another series of visits. On 7 May she visited the center of DR3. This northeasterly movement with return on 8 May was especially interesting since there were no active drummers in that area but a tree planting crew using a tractor was there. I think that her movement to within a few feet of this operation represented a response to a false stimulus, the tractor, which was roughly analogous to that of a response to drumming. Bump et al. (1947, p. 263–264) report several instances where grouse, of unspecified sex, responded to tractor and wood chopping sounds. A final overt response to drumming activity occurred the following day (9 May) when she moved eastward and remained overnight within the activity center of DR4. On 10 May she returned to the habitat in which she was to nest. Indications are that the first egg was laid on that date.

Also, indications are that oestrus began seven days prior (3 May) to the first egg and ended the day before. Calculated oestrous dates and egg laying rates as described in Bump et al. (op. cit.) seem reasonably valid when applied to hen number 1826.

According to Bump et al. (op. cit., p. 267) oestrus in captives ceases almost im-

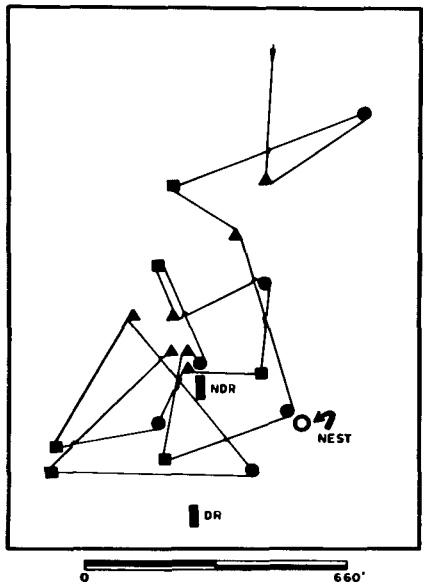

FIG. 2. Immature female, No. 1828. Movements and locations during oestrus, 4–11 May. The 4 May movement is from the north (arrow). DR and black rectangle indicate a drumming male while NDR indicates a less persistent drummer. Other symbols are as in Fig. 1.

mediately after copulation. Assuming that wild grouse react similarly, I interpret the mating behavior of hen No. 1826 as follows: (1) oestrus, per se, commenced on 6 May; she responded to a drumming male on that date but did not copulate; (2) she responded to another male on 7 May and again did not copulate; (3) she responded to a false stimulus on 8 May; (4) successful copulation occurred on 9 May after she had responded to the third male within her range. This hen, without question, was attracted to the activity centers of drumming cocks, and sounds produced by the cocks were the proximate stimuli which elicited her response. The pair-bond was transitory, probably of a duration no longer than a few hours. Because the cocks continued to drum after the hen had left their respective activity centers and, I presume, continued to attract hens, this mating behavior is properly termed *promiscuous*. Even if the assumption of a single copulation were not warranted, the behavior remains promiscuous.

Hen No. 1828.—The mating season for this bird was foreshadowed on the morning of 25 April when she moved toward the sound of drumming activity. However she remained within her tightly defined winter range (7 acres) until 4 May. Figure 2 shows her movements from that date through the oestrous season.

She moved into a drumming activity center on 6 May and it seems certain that oestrus commenced on that date. Her movements indicated a responsiveness to drumming at least through 10 May. The persistent drumming of an adult cock (DR, Fig. 2) probably signaled the hen's departure from the winter range, but a much less persistent drummer (NDR) along her path of movement may have secured her attention also.

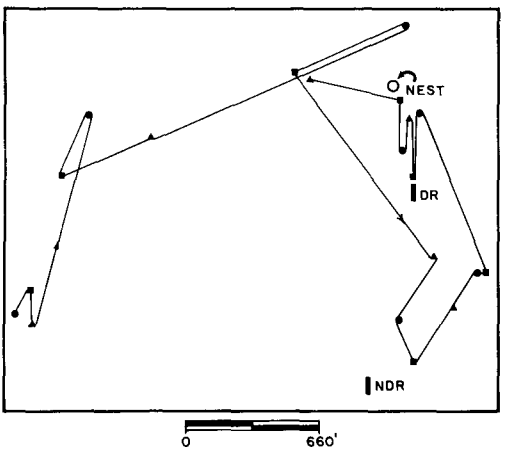

FIG. 3. Immature female, No. 1944. Movements and locations during oestrus, 4–11 May. The 4 May location is in the southwestern part of the figure. See Fig. 1 for explanation of symbols.

I interpret her mating behavior as follows: (1) oestrus, per se, commenced on 6 May; (2) copulation probably occurred on 9 or 10 May. This hen, as with number 1826, was unquestionably attracted by the sound of a drumming cock. While the map of her movements and locations during the oestrous period may suggest a pair-bond of some duration, particularly with NDR, observations during that period indicated that lengthy juxtaposition of the sexes was circumstantial. Because the cocks continued to drum after the hen had established her nest, this behavior was promiscuous.

Hen No. 1944.—Hen number 1944 was radio-marked on 26 April. An overt response to drumming was noted on 29 April when she moved toward an activity center which included two males. Another precursory response was noted on 1 May. Figure 3 shows her movements from 4 May through the oestrous period.

The long movement to the northeast and into the range of a drumming male (DR in Fig. 3) probably marked the first day of oestrus; which was identical with the postulated onset date for hens 1826 and 1828—6 May. After spending two days within audible range of the drummer, she returned to his activity center on 9 May and then into her nesting habitat on 10 May. A "non-drumming" male (NDR, Fig. 3) might have influenced the hen's movements, but I was reasonably sure that this did not occur.

The mating behavior of hen No. 1944 is interpreted as follows: (1) oestrus, per se, commenced on 6 May; (2) copulation probably occurred on 9 or 10 May.

As with the other hens, No. 1944 was attracted by the sound of drumming to the activity center of a cock. No more than a transitory pair-bond developed and the behavior of both cock and hen indicated promiscuous mating.

DISCUSSION

A basic question on the behavior of Ruffed Grouse was answered when hens were observed responding positively to drumming cocks. The question of the duration of the pair-bond was not answered conclusively, but the

TABLE 2
PATTERNS OF MATING BEHAVIOR IN FEMALES AS RELATED TO TIME

Bird number	Behavior pattern			
	Pre-oestrus		Oestrus	
	Adumbration	Prelude	Mating	Copulation
1826	25 April	1 May	6 May	9 May
1828	25 April	4 May	6 May	9 or 10 May
1944	?	24 April	6 May	9 or 10 May

evidence is highly suggestive that the sexes meet solely for copulation and that the mode of sexuality is promiscuous.

Promiscuity is a generic term which does not adequately depict the intricate pattern made manifest in the movements of the three hens. Actually, four *levels* of response are apparent in the pattern and these I term: *adumbration*: passive restlessness to drumming; *prelude*: overt restlessness to drumming; *mating*: proximal movement; *copulation*: nidification. Mating and copulatory phases comprise oestrus per se.

Onset dates for each of the phases are given in Table 2. The patterns of responsiveness for the hens are strikingly similar and suggest that stimuli, internal and external, are also arranged in a precise pattern. There is other evidence that this is so. Data provided by Gullion (unpublished MS.) from a four-year study, also at Cloquet, Minnesota, indicate that the period of most intensive drumming activity is precisely fixed in time. In his study, males exposed to extremely variable annual meteorological and phytophenological conditions still reached a peak in their drumming activity within 3 days of 29 April. The peak was on 26 April in 1963, which coincides with the adumbration phase of the behavior that I describe.

An inflexible pattern of mating has adaptive significance for birds faced with extremes in wintering conditions. The periods of net loss in energy storage must be balanced in the animal by periods of net gain. For northern species these periods are rather rigidly fixed. The stress of winter begins in early November, ends in early April, and is followed in quick order by the stresses of mating, egg-laying, incubation, and care of young. Except for a brief respite in April, these all may be periods of net losses in energy. A scant two to three months remain for the hen to recoup her losses. Therefore, a prolonged mating season becomes a luxury ill-afforded to endemic northern species, and an inflexible breeding season which results from rigid behavioral patterns should not be unexpected in the Ruffed Grouse of northern Minnesota.

SUMMARY

A radio-telemetric system was used to obtain data on sexual relationships in the Ruffed Grouse. The hen was attracted to the site of the cock's drumming performance but no more than a transitory pair-bond developed. A promiscuous mating habit was indicated.

The movements of hens suggested varying levels of response to the stimuli of mating, and responses were precisely fixed among hens and in time. Such an inflexible pattern of mating has adaptive significance for Ruffed Grouse which winter in the rigorous climate of northern Minnesota.

ACKNOWLEDGMENT

This paper is a contribution from a project supported by National Science Foundation Grant No. GB-1345. The data from the current research on Ruffed Grouse at the Cloquet Forest Research Center and the techniques developed therein were essential to this project. William H. Marshall and Gordon W. Gullion provided these data and participated in many ways during the field work. Phillip Schladweiler, James Forbes, and David Peterson were able field assistants. Frederick Greeley and David K. Wetherbee offered valuable criticism of the manuscript.

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NEW LIFE MEMBER

Dr. Donald J. Borror, of Columbus, Ohio is a new Life Member of The Wilson Ornithological Society. Dr. Borror holds degrees from Otterbein College, and The Ohio State University, and is currently Professor of Zoology and Entomology at Ohio State. Ornithologists know Dr. Borror as one of the pioneers in the recording of bird songs and the analysis of these recordings by audiospectrographic means. He is the author of numerous papers on bio-acoustics, and has also published several phonograph records of bird songs. He has also co-authored a popular textbook in entomology, and has published many papers on that subject. He is a member of the AOU, the Entomological Society of America, Society of Systematic Zoology, and the American Association for the Advancement of Science. Dr. Borror is married, and has one son, who following in his father's footsteps, is a professor of zoology.