ACTIVITY, HOME RANGE, AND HABITAT USAGE OF
FEMALE RUFFED GROUSE DURING THE EGG-LAYING, INCUBATION,
AND EARLY BROOD PERIODS AS DETERMINED BY RADIOTELEMETRY

STEPHEN JOHN MAXSON

DECEMBER, 1974

MASTER

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FEMALE RUFFED GROUSE DURING THE EGG-LAYING, INCUBATION,
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BY
STEPHEN JOHN MAXSON

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INTRODUCTION

The Ruffed Grouse (Bonasa umbellus) is an important game species throughout its range and has received considerable attention from researchers, e.g., Bump et al. (1947), Edminster (1947), Gullion and Marshall (1968), and others. Since this usually wary species often inhabits dense forests, prolonged observations of individuals are difficult and relatively few precise data have been obtained on certain aspects of its life cycle. In recent years radio-telemetry techniques have greatly increased our knowledge of the movements and behavior of individual birds especially in Minnesota. Such data are available from the Cloquet Forest Research Center, e.g., Barrett (1970), Brander (1965, 1967), Godfrey (1967), Godfrey and Marshall (1969), Marshall (1965), and Schladweiler (1965, 1968). At the Cedar Creek Natural History Area intensive studies have been made by Archibald (1973) and Huempfer (unpublished data). However, a number of questions concerning activity and behavior of female grouse during the breeding season remain unanswered.

The objectives of this study were to determine the activity periods, home range, and habitat usage of individual female Ruffed Grouse during the egg-laying, incubation, and post-incubation periods. Field observations were made from 1 April through 30 June, 1971, and 1 April through 7 July, 1972. Most of the field work took place within a 617 acre area in the west-central portion of the University of Minnesota's Cedar Creek Natural History Area in Anoka and Isanti Counties, about 30 miles north of Minneapolis, Minnesota. Many aspects of the Cedar Creek area

have been described in detail by Pierce (1954). Plant species have been listed recently by Moore (1973). In general, the topography is flat to slightly rolling with sandy upland areas dominated by oak forests and old fields interspersed with lowlands of peat or muck soils dominated by white cedar, tamarack, and alder. Cedar Creek habitats are described in greater detail in the Results section below.

METHODS

Capture and Marking Techniques

Female Ruffed Grouse were captured by baited lily-pad traps (Gullion, 1965), nest traps (Weller, 1957), dip-netting on the nest (Robel et al., 1970) and by nightlighting (Huempfer, unpublished data). Selected locations were baited with shelled corn dyed with Rhodamine B (Allied Chemical Corporation, National Aniline Division) for periods of a few days to several weeks. Lily-pad traps, used during the pre-incubation period, were placed at bait sites utilized the most by grouse. Usually these traps were set one to two hours before sunset and checked shortly after dark. As grouse are not nocturnal, the traps were left set overnight and checked one to two hours after sunrise the following morning. Since any unnecessary capture increases the possibility of injury to a bird, a trap was moved to a new location when recaptures began to occur at a particular site. All lily-pad traps had been removed from the field by 30 April, 1971, and 14 April, 1972. Nest trapping was used only during the last week of

incubation. Nightlighting was employed during the pre- and post-incubation periods in recapturing several birds for transmitter battery changes. After a grouse had roosted for the night, its location was determined by triangulation of radio signals received by the two towers of the Cedar Creek automatic radio-tracking system (Cochran et al., 1965). The nightlighting crew, usually consisting of two dip-net carriers, two spotlight operators (motorcycle battery operated, backpack mounted) and one portable radio receiver operator then moved to the approximate location of the roosted grouse. The receiver operator located the bird, the spotlights were directed at it and a netting attempt was made. If the bird escaped, it was relocated by the receiver operator and another capture attempt was made. In most instances birds were captured on the first or second attempt.

Hens captured on their nests were handled in the field to minimize the time these birds were kept off the eggs. All others were placed in burlap bags and transported to the Cedar Creek laboratory where they were weighed, sexed, aged, leg-banded, and equipped with radio transmitters. Any injuries sustained by the birds were noted at this time. Grouse were aged by comparing the amount of sheathing at the base of the 8th and 9th primaries (Davis, 1969) and sexed by noting the length of the central retrix (Dorney and Holzer, 1957; Gullion, 1964).

Grouse were fitted with a modified version of a transmitter described by Cochran and Lord (1963) and weighing 24-26 grams. The transmitter harness was similar in design to one described by

Brander (1968). The radio components and battery (12 gram Mallory RM1) of the transmitter were coated with a dental acrylic material (Perm, Hygienic Dental Manufacturing Co.). A 9-inch stainless steel whip antenna (0.020 in. diam.) was contained within a teflon tube sealed at the end with beeswax. Transmitters broadcasted continuous signals, each at a different frequency in the 53 mHz range. Expected transmitter life ranged from 50 to 75 days but usually birds were refitted with new transmitters before this time. All birds were released at the point of capture.

Data Recording Techniques

Location

Radio-marked grouse were monitored with an automatic radio-tracking system (Cochran et al., 1965). Two towers 1/2 mile apart support directional receiving antennas continually rotating at 1-1/3 rpm. During each antenna revolution, radio signals emanating from the transmitted grouse were received by the antennas. The signals were relayed to a centrally located laboratory and, after amplification and modification, were recorded on 16 mm film as degree bearings for each tower which were used to determine the location of the bird by triangulation. With the use of a microfilm reader, a technician was able to determine tower bearings for each bird to the nearest degree at 15 minute intervals, or as closely as possible to this interval, throughout the day.

Cochran et al. (1965), Sargeant et al. (1965), Heezen and Tester (1967) and Tester (1971) discussed the accuracy limitations and possible errors associated with use of this system. In any animal-location system based on triangulation, discrepancies occur between the plotted location and the true location of the animal. These vary according to the distance and direction of the animal from the towers. Cochran et al. (1965) determined the accuracy of the system to be plus or minus 0.5 degrees on windy days and plus or minus 0.3 degrees on calm days. Heezen and Tester (1967) described error polygons (a figure indicating the area within which an animal could be located for a particular plotted location) and showed how the size and shape of these figures varied in relation to distance and direction from the towers. Sargeant et al. (1965) classified the Cedar Creek area into accuracy zones. All grouse monitored during this study were within the 200 foot zone. This means that if a one-degree error occurred, it would give a plotted location no more than 200 feet from the true location of the bird. Sargeant et al. (1965) found that for red foxes, the average distance error for 39 locations within this zone was 79 feet.

Activity

An activity code (active, inactive, unknown) was determined at 15 minute intervals for each bird. Marshall and Kupa (1963) determined that the pitch of the radio signal changed as a grouse moved about. This change in signal pitch associated with activity

is reflected as irregularities in signal peaks on the film record (Sargeant et al., 1965). During each 15 minute period (except during incubation) a grouse was considered active if 4 or more signals exhibited these irregularities, or if a change in bearing of one or more degrees for either tower occurred. During the incubation period activity changes were determined to the nearest minute.

Weather and Plant Phenology

During both years, weather data were recorded by the U.S. Weather Bureau station located at the Cedar Creek Natural History Area. Phenological events also were recorded. In 1971 detailed phenological data were collected for trembling aspen (Populus tremuloides) (McColl and Maxson, unpublished data). Less detailed data were taken for other species. In 1972, in addition to a general recording of events, a selected site in each of six different habitats was photographed once a week during the study period. Thus, a permanent visual record was obtained of phenologic changes both within and between habitat types.

Data Analysis

Activity and location data were analyzed with the University of Minnesota's Control Data 6600 computer system. These data were sorted in chronological order and checked for errors. Following error corrections, the tower degree bearings were converted to

X-Y coordinates (Siniff and Tester, 1965). Activity data were divided into pre-incubation, incubation, and post-incubation periods. Location data were divided into pre-egg-laying, egg-laying, incubation, and 7-day periods after incubation continuing through the end of the study period.

Activity

Activity data for each bird were analyzed in two ways. First, the sampled activity for each day was plotted giving each 15-minute interval an activity symbol (active, inactive, unknown). This illustrated day to day periods of activity. Second, the percentage of times a bird was active during each 15-minute interval for a given time period (pre-incubation, incubation, post-incubation) was plotted. A composite 24-hour day comprised of data for all days during a time period was thus formed to illustrate activity trends throughout the specified period.

Location

For analysis of location data, the study area was divided into a grid of 0.092 acre squares (60.2 feet on a side). Each location of a grouse during a given time period was assigned to the appropriate grid square. When one or more "fixes" (animal locations) fell within a grid square, it was assumed that the entire square was utilized by the bird. This square size was used primarily because computer drawn home range maps of this scale could be overlaid directly on a map (scale 1 in. = 200 ft.)

coded for vegetation types. This square size also seemed reasonable considering the accuracy limitations of the radio-tracking system.

In calculating the size of a bird's home range, the area within each occupied grid square plus certain unoccupied squares was summed. Squares containing no fixes were included in the home range if the following criteria were met: 1) if two occupied squares were separated in a horizontal or vertical direction by three or fewer empty squares, the empty squares were included in the home range, 2) if two occupied squares were separated in space by 0.08 miles or less and in time by 20 minutes or less, a straight line of travel between the two squares was assumed and all empty squares falling along that line were included in the home range. All empty squares thus added to the home range were assumed to have been used by the bird. Fixes falling in squares separated from the nearest occupied square by four or more empty squares, and also not meeting the second criterion above, were considered to be erroneous in most instances and eliminated.

Home ranges were also calculated using the minimum-area method (Mohr, 1947) in which all peripheral locations of a bird were connected with straight lines. In this case the area within the resulting n-sided polygon constituted the bird's home range.

Cumulative home ranges were calculated to determine whether birds were using the same area in succeeding time periods, or if they were moving into new areas. Using the grid system described

above, a bird's home range map for a given time period was overlaid on maps for all preceding periods. All grid squares within that home range, but not previously occupied by the grouse were added to the total home range. A wide ranging individual continually using new areas exhibited a rapidly increasing cumulative home range whereas a more sedentary individual using primarily the same area during succeeding time periods exhibited little increase in cumulative range size.

Vegetation Analysis

Largely through the efforts of Mr. Richard Huempfner, vegetation types on the study area were determined in the field with the aid of aerial photographs. Data obtained from this work were transferred to an aerial photo map (scale 1 in. = 200 ft.) of the Cedar Creek area. The vegetation map was then overlaid with home range maps for each bird. The number of grid squares within the home range occurring in each habitat type was determined as well as the number of fixes falling in each habitat type. In cases where several habitat types were present, the grid square was given the vegetation code of the habitat comprising the largest portion of the square. The percentage of each habitat type within a bird's home range and the percentage of fixes falling in each habitat type were calculated from these data.

An area of 617 acres was defined to determine the availability of the various habitat types to radio-marked grouse. This area included the home ranges of all transmitted female grouse. The

percentage of each habitat type within the 617 acres was calculated.

Field Observations

Nests

One to five persons made systematic searches for nests of unmarked hens both years, resulting in six nests being found in 1971 but none in 1972, although the search effort was about the same each year. The six unmarked hens were nest trapped and fitted with transmitters.

Nests of incubating radio-marked hens were located with a hand-held portable receiver to determine clutch sizes. Following hatching or nest destruction, all nest sites were permanently marked. Habitat analysis was carried out the following spring at the approximate time of nest initiation. Each site was photographed, solid objects near nests were noted, and distances between nests and the nearest aspen trees recorded.

Egg-Laying

By reviewing the telemetry record after a nest was located, it was possible to determine when the hen had visited the nest site prior to the onset of incubation. The egg-laying rhythm was determined from these data.

TV Observations of an Incubating Hen

During the 1972 season a small TV camera was placed near the

nest of No. 2219 for 16 days. A TV monitor in the laboratory made possible day time observations of this bird's incubation behavior.

Location of Hens During Nest Absences

Radio-marked incubating hens were located with a portable receiver while away from their nests to determine exact feeding locations. This practice was discontinued after emerging foliage made observations of birds at feeding sites virtually impossible.

Brood Flushes

Marked hens with broods were field located and flushed at approximately one week intervals in an attempt to count the number of surviving chicks and observe the reaction of hens to a potential predator.

Captive Brood

Incubating hen No. 1697 was killed by a predator on 29 May, 1971, several days before its eggs were due to hatch. Examination of one of the abandoned eggs disclosed a live embryo despite the fact that the eggs had not been attended for about 24 hours following predation of the hen. Nine of the 10 remaining eggs placed in an incubator hatched on 1 June. At first the chicks were kept in a cardboard box placed under a brooder lamp. They were fed live insects caught with a net. When 1 week old they were moved to an outdoor wire enclosure during the day. All were

color banded at 2 weeks and thereafter weighed weekly throughout the remainder of the summer. When 5 weeks old they were moved to a large outdoor enclosure. Notes on their behavior were recorded regularly for a few days following hatching, and irregularly thereafter.

RESULTS

Ruffed Grouse populations were at a high or peak level at Cedar Creek during the study. Thirty and 28 drumming males were located in an approximately one-square-mile area in 1971 and 1972 respectively (Huempfer, unpublished data). His area was almost identical to the 617 acre area of the present study.

Capture and Transmission Data

Twenty-two female Ruffed Grouse were captured and equipped with radio transmitters. Table 1 summarizes capture data for these birds including captures occurring outside the study period. Weights of the birds fluctuated between captures and generally decreased during the nesting period, reflecting the physiological stress of egg-laying and incubation.

Two types of minor injuries occasionally occurred during captures. Beaking, which resulted in the base of the upper mandible being rubbed raw, developed when the birds poked their heads through the wire of lily-pad traps. Injuries of this type usually healed rapidly. At times, a slight skin abrasion at the wrist joint developed when a bird attempted to escape the trap,

Table 1. Capture data for female Ruffed Grouse.

Bird No.	Age	Date of Capture	Method of Capture	Bird Weight (grams)	Injuries and Remarks
1657	J	10 Apr 71	Lily-pad	548	None
		29 May 71	Nest trap	460	None
1684	A	2 Mar 71	Lily-pad	576	Slight beaking
		1 May 71	Night-lighted	551	None
1689	J	3 Apr 71	Lily-pad	490	None
		20 Apr 71	Lily-pad	513	Severely scalped
		21 May 71	Found dead	430	-
1690	J	6 Apr 71	Lily-pad	610	Slight scalping; captured with 1691
1691	A	6 Apr 71	Lily-pad	607	Slight beaking; captured with 1690
		31 May 71	Nest trap	470	Beaked
		3 Aug 71	Night-lighted	472	None
		21 Oct 71	Night-lighted	535	None
		25 Jan 72	Snow burrow netted	499	None
1695	J	13 Apr 71	Lily-pad	527	None
		9 Jun 71	Nest trap	448	None
1697	J	26 May 71	Nest trap	473	None

Table 1. Capture data for female Ruffed Grouse (continued)

Bird No.	Age	Date of Capture	Method of Capture	Bird Weight (grams)	Injuries and Remarks
1698	J	27 May 71	Nest trap	426	Abrasion on right wrist
		27 Jul 71	Night-lighted	459	None
		12 Oct 71	Night-lighted	501	None
		22 Dec 71	Night-lighted	485	None
1699	J	27 May 71	Dip-netted on nest	507	None
2200	A	28 May 71	Nest trap	490	None
		21 Jul 71	Night-lighted	448	None
2201	J	31 May 71	Nest trap	534	None
		27 Jul 71	Night-lighted	529	None
2202	?	2 Jun 71	Nest trap	459	None
		3 Aug 71	Night-lighted	432	None
2210	J	5 Nov 71	Lily-pad	607	Beaked
		22 Feb 72	Snow burrow netted	532	None
2219	J	15 Nov 71	Lily-pad	536	None
		4 Mar 72	Snow burrow netted	478	None
		30 May 72	Nest trap	464	None
2224	J	21 Nov 71	Lily-pad	573	Slight beaking
		11 Apr 72	Mist net	533	Probable muscle strain from capture
		4 May 72	Night-lighted	511	None; did not fly during capture attempt
		8 Jun 72	Nest trap	383	None

Table 1. Capture data for female Ruffed Grouse (continued)

Bird No.	Age	Date of Capture	Method of Capture	Bird Weight (grams)	Injuries and Remarks
2235	A	2 Feb 72	Snow burrow netted	535	None; leg banded only
		5 Apr 72	Mist net	532	None; transmitter attached
		1 Jun 72	Nest trap	482	None
		9 Aug 72	Night-lighted	483	None
2238	J	28 Mar 72	Lily-pad	567	None
		3 Apr 72	Lily-pad	512	Slight abrasion at wrists
		6 Jun 72	Nest trap	469	Slight abrasion at wrists
2239	J	29 Mar 72	Lily-pad	494	None
		7 Apr 72	Lily-pad	527	None
		31 May 72	Nest trap	450	Tips of primaries #7, 8, 9 broken (left wing)
2241	J	2 Apr 72	Lily-pad	544	None
		22 Jun 72	Night-lighted	483	None
		21 Sep 72	Night-lighted	538	Bare spot on back under transmitter; Healed callous under left wing
		13 Oct 72	Lily-pad	573	Slight beaking
2245	A	7 Apr 72	Lily-pad	501	Flew weakly when released
		6 Jun 72	Nest trap	484	Flew weakly when released
		23 Aug 72	Night-lighted	519	None
2246	A	7 Apr 72	Lily-pad	612	Very slight beaking
2248	J	14 Apr 72	Lily-pad	565	Slight beaking
		9 Jun 72	Nest trap	483	Slight abrasion at wrists

but this injury healed rapidly and did not appear to hinder flight.

Serious trapping injuries befell 2, possibly 3 hens. Hen 1689 was severely scalped in a lily-pad trap. It survived the head injury only to succumb to a late-season snowstorm one month later, so far as could be determined. Examination of the carcass disclosed a fully developed egg in the oviduct. Hen 2224 was accidentally captured in a mist net set for captors and apparently suffered injury to the flight muscles. It was reluctant to fly and when flushed flew weakly a short distance only. The unusually low weight of this bird when nest trapped was indicative of its poor condition. Hen 2245 also may have suffered muscle strain. It was captured twice during the study and flew weakly when released each time. Data from these 3 hens were not used in the analysis.

Birds were monitored for periods ranging from 4 to 98 days during the study, and up to 324 days including all time periods monitored (Table 2).

Nesting Data

Nesting data for all birds except Hen 1689 are summarized in Table 3. Due to the injured condition of Hens 2224 and 2245 their clutch sizes were not used in calculating the mean clutch size. Data from two nests of unmarked hens located during 1973 were included. Dates of "oestrus" (a term normally applied to mammals, but used here because it appears frequently in

Table 2. Transmission data for female Ruffed Grouse.

Bird No.	Total Time on System	Total Days Monitored	Time on Tracking System during Study Period	No. Days	Reason for Signal Termination
1657	11 Apr 71-25 Jul 71	106	11 Apr 71-30 Jun 71	81	predator kill (avian)*
1684	3 Mar 71-20 May 71	79	1 Apr 71-20 May 71	50	predator kill (mammal)
1689	4 Apr 71-20 May 71	47	4 Apr 71-20 May 71	47	died (head injury)
1690	7 Apr 71-11 Jun 71	66	7 Apr 71-11 Jun 71	66	predator kill (mammal)*
1691	7 Apr 71- 1 Feb 72	301	7 Apr 71-30 Jun 71	85	predator kill (avian)
1695	14 Apr 71-24 Jun 71	72	14 Apr 71-24 Jun 71	72	predator kill (avian)*
1697	26 May 71-20 May 71	4	26 May 71-20 May 71	4	predator kill (avian)
1698	27 May 71-23 Dec 71	211	27 May 71-30 Jun 71	35	predator kill (avian)
1699	27 May 71- 7 Jun 71	12	27 May 71- 7 Jun 71	12	predator kill (mammal)
2200	28 May 71- 1 Sep 71	97	28 May 71-30 Jun 71	34	predator kill (avian)
2201	1 Jun 71- 4 Oct 71	126	1 Jun 71-30 Jun 71	30	hunter kill
2202	2 Jun 71- 6 Aug 71	66	2 Jun 71-30 Jun 71	29	predator kill (avian)

* leg caught in transmitter harness

Table 2. Transmission data for female Ruffed Grouse (continued)

Bird No.	Total Time on System	Total Days Monitored	Time on Tracking System during Study Period	No. Days	Reason for Signal Termination
2210	6 Nov 71-25 May 72	202	1 Apr 72-25 May 72	55	predator kill (avian)
2219	16 Nov 71- 4 Oct 72	324	1 Apr 72- 7 Jul 72	98	battery failure
2224	21 Nov 71-13 Jun 72	203	12 Apr 72-13 Jun 72	63	predator kill (avian)
2235	6 Apr 72-27 Oct 72	205	6 Apr 72- 7 Jul 72	93	battery failure
2238	29 Mar 72-21 Jun 72	85	1 Apr 72-21 Jun 72	82	predator kill (avian)
2239	30 Mar 72- 6 Jul 72	99	1 Apr 72- 6 Jul 72	97	predator kill (avian)
2241	3 Apr 72-14 Oct 72	195	3 Apr 72- 7 Jul 72	96	predator kill (mammal)
2245	8 Apr 72-23 Oct 72	199	8 Apr 72- 7 Jul 72	91	battery failure
2246	8 Apr 72-25 Jun 72	79	8 Apr 72-25 Jun 72	79	battery failure
2248	15 Apr 72-12 Jun 72	59	15 Apr 72-12 Jun 72	59	predator kill (avian)

Table 3. Nesting Data

Bird No.	Calculated Dates of "Oestrus"	Date of First Egg	Egg-Laying Period (Days)	Clutch Size	Incubation Onset	Incubation Period (Days)	Hatch Date	No. Eggs Hatched	Remarks
1657	17-21Apr71	24Apr71*	14*	11	08:50 8May71	26	3Jun71	11	Left nest approx. 08:45 3Jun71
1684	12-16Apr71	19Apr71	14*	10	2May71	-	-	-	Killed by predator, 20May.
1690	21-25Apr71	28Apr71	15	10	09:40 12May71	24	5Jun71	10	Left nest approx. 10:15, 5Jun71.
1691	16-20Apr71	23Apr71	19	12	10:46 11May71	25	5Jun71	12	Left nest approx. 09:16, 5Jun71.
1695	18-22Apr71	25Apr71	25	8	09:17 20May71	24	13Jun71	8	Left nest approx. 11:36, 13Jun71.
1697	17-21Apr71	24Apr71*	15*	11	8May71*	24*	1Jun71	9	Killed by pred. 28May71 Eggs hatched in incubator.
1698	-	-	-	11	-	-	-	-	Nest destroyed approx. 06:46, 2Jun71.
1699	14-18Apr71	21Apr71*	17*	12	7May71*	24*	30May71	11	Left nest approx. 14:30 30May71, 1 egg addled.

Table 3. Nesting Data (continued).

Bird No.	Calculated Dates of "Oestrus"	Date of First Egg *	Egg-Laying Period (Days)	Clutch Size	Incubation Onset	Incubation Period (Days)	Hatch Date	No. Eggs Hatched	Remarks
2200	16-20Apr71	23Apr71	17*	13	9May71*	24*	1Jun71	12	Left nest approx. 15:01, 1Jun71, 1 egg cracked, removed by hen before hatch.
2201	-	-	-	7	-	-	-	-	Eggs pipped, 31May71. Nest destroyed, 1Jun71.
2202	-	-	-	8	-	-	-	-	Nest destroyed approx. 13:20, 13Jun71.
2210	22-26Apr72	29Apr72	17	12	11:01 15May72	-	-	-	Killed by pred. 24May72.
2219	24-28Apr72	1May72	14	11	06:00 14May72	26	8Jun72	2	Nest destroyed approx. 04:00, 2Jun72, 2 eggs hatched in incubator.
2224	-	-	-	6	-	-	-	6	Hen injured. Data probably invalid.
2235	20-24Apr72	27Apr72*	17*	12	04:42 13May72	24	6Jun72	10	Left nest approx. 06:46, 6Jun72, 2 eggs added.
2238	23-27Apr72	30Apr72	17	13	20:01 16May72	25	10Jun72	11	Left nest approx. 14:06 10Jun72, 2 eggs added.

Table 3. Nesting Data (continued)

Bird No.	Calculated Dates of "Oestrus"	Date of First Egg	Egg-Laying Period (Days)	Clutch Size	Incubation Onset	Incubation Period (Days)	Hatch Date	No. Eggs Hatched	Remarks
2239	23-27Apr72	30Apr72	14	10	13:35 13May72	25	7Jun72	9	Left nest approx. 11:00, 7Jun72. 1 egg added.
2241	17-21Apr72	24Apr72	17	13	06:31 10May72	-	-	-	Nest destroyed approx. 03:38, 26May72.
2245	-	-	-	10	-	-	-	-	Nest destroyed, 8Jun72.
2246	21-25Apr72	28Apr72	17	13	05:01 14May72	25	8Jun72	13	Left nest approx. 10:38, 8Jun72.
2248	26-30Apr72	3May72*	17*	12	05:16	24	12Jun72	12	Left nest approx. 18:25, 12Jun72.
"A"	14-18Apr73	21Apr73*	14*	11	4May73*	24*	27May73	11	Hen unmarked.
"B"	17-21Apr73	24Apr73*	19*	14	12May73*	24*	4Jun73	14	Hen unmarked.

*These data calculated e.g., Egg-Laying period-- 10-11 eggs = 14 days, 12-13 eggs = 17 days;
Incubation period = 24 days.

literature on Ruffed Grouse) were calculated by backdating 3-7 days prior to laying of the first egg (Bump et al., 1947).

For 8 hens, from which nearly continuous data were obtained, the date of laying of the first egg was determined by backdating through the film record which showed when the hen was at the nest. The egg laying rhythm will be discussed later in detail. Bump et al. (1947) reported an average egg laying rate of 2 eggs every 3 days. Kupa (1966) found a laying rate of .67 eggs per day. Barrett (1970) reported laying rates of 9 eggs in 10 days and 10 eggs in 14 days for 2 nests. Although some individual variation was evident in the present study, the determined rates of egg laying were generally somewhat faster than reported by Bump et al. (1947). For 9 hens whose date of incubation onset could be determined, the egg laying rates were calculated (Table 3) based on the rates determined in this study, i.e., 10-11 eggs = 14 days and 12-13 eggs = 17 days.

Clutch size ranging from 7-14 eggs (average 11.1) were comparable to the findings of other researchers, e.g., Bump et al., 1947 - 11.5; Fallis and Hope, 1950 - 12.2; Kupa, 1966 - 9.9; Rusch and Keith, 1971 - 11.6; Cringan, 1970 - 11.4.

Nests of juvenile Hen 1695 and Hen 2202 (age unknown) were probably renests in that they were started late and had small clutches (Table 3). Although juvenile Hen 2201 did not nest late, her clutch was unusually small, suggesting that it may have been a repeated attempt. Bump et al. (1947) and Edminster (1947) discuss reneesting in Ruffed Grouse, although these authors

apparently did not have marked individuals at their disposal. Clutch sizes for their presumed renesting birds averaged 7.5 and 7.9 eggs respectively. Cringan (1970) assumed that late hatching clutches, which averaged 8.5 eggs, were renests. Porath and Vohs (1972) state that renesting has not been convincingly proven. However, Barrett (1970) reported that a radio-marked juvenile hen, which had lost its first clutch of 4 eggs to a predator, prior to incubation onset, laid a second clutch of 4 eggs.

In any event, the Ruffed Grouse usually does not renest. Bump et al. (1947) state that the time a first nest is destroyed largely determines whether a hen will renest. They further state that once the first clutch has been incubated several days, chances of renesting are greatly reduced. Data from the present study substantiate those of Bump et al. None of 6 incubating hens attempted to renest following loss of their clutches.

Incubation periods, i.e. the interval from the onset of incubation until the hen left the nest with the brood, ranged from 24 to 26 days. Bump et al. (1947) reported an average incubation period of 23.5 days under game-farm conditions. Barrett (1970) reported incubation periods of 24 and 25 days for 2 nests, and Schladweiler (1965) recorded a 26-day incubation period for one nest. Variation in incubation periods may be a result of differing weather conditions (temperature and precipitation) as well as the amount of disturbance to the nesting bird, which lowers egg temperatures and retards embryonic development. Breckenridge (1956) stated that although the incubation period

of a species cannot be shorter than a certain minimum period, it may be greatly extended due to severe chilling of the eggs.

Nest failure was similar during both years of the study. In 1971 2 hens were killed by predators during incubation while 3 had clutches destroyed. One hen was killed and 3 clutches destroyed in 1972. The overall hatching success for all nests was 59%, which is similar to the figure of 61% reported by Bump et al. (1947). Gullion (1970) stated that normally 68% of the eggs laid could be expected to hatch while Rusch and Keith (1971b) found that approximately 50% of hens alive in spring produced broods.

Hatching dates at Cedar Creek averaged four days later in 1972 (8 June) than in 1971 (4 June).

There appears to be a general tendency for nests of the Ruffed Grouse to hatch slightly earlier in the more southerly portions of its range than in localities further north. Porath and Vohs (1972) reported the peak of hatching occurred during the last week of May in northeastern Iowa. Bump et al. (1947) stated that most nests in New York hatched during the last week of May and the first week of June. Cringan (1970) recorded mean hatching dates from 29 May - 4 June during 1964-1969 in southern Ontario. Hale and Wendt (1951) reported 61% of 42 broods hatching between 27 May - 9 June in northern Wisconsin, whereas Thompson (1958) reported average Wisconsin hatching dates from 1 June - 10 June during 1952-1957. Kupa (1966) stated that nests at Cloquet, Minnesota, hatched between 4 June and 20 June with

75% hatching by 12 June,

Activity

Data periods for analysis of activity are indicated in Table 4. Table 5 summarizes the percentage of time the birds were determined to be active during the pre-incubation, incubation, and post-incubation periods. Although individual variation existed during a given period, mean values between periods indicate general trends. Percent activity tended to be greater during the post-incubation period than the pre-incubation period. This may have been due to increased day length. Hens with broods tended to be less active than those without broods. During incubation, activity was much reduced and limited to a few short feeding periods each day.

Pre-Incubation

The temporal distribution of percentage of 15-minute intervals active for 9 hens during the pre-incubation period is illustrated in Figure 1a, b, c. Activity seldom occurred at night. Peaks of activity were closely associated with sunrise and sunset. This pattern is similar to the two peak activity patterns reported for several species of day-active birds by Aschoff (1966). The evening peak was higher than the morning peak for all hens. Archibald (1973) found a similar relationship between dawn-dusk activity peaks for male grouse during spring and Pierson and Tester (unpublished data) noted a similar pattern.

Table 4. Data periods for analysis of activity.

Bird No.	Inclusive Dates	No. Days	Time Period
1657	08:00, 11 Apr - 09:49, 8 May 71	28	Pre-incubation
	09:50, 8 May - 08:45, 3 Jun 71	27	Incubation
	08:46, 3 Jun - 23:59, 21 Jun 71	20	Post-incubation
1690	11:30, 7 Apr - 09:39, 12 May 71	36	Pre-incubation
	09:40, 12 May - 10:15, 5 Jun 71	25	Incubation
1691	11:23, 7 Apr - 10:45, 11 May 71	35	Pre-incubation
	10:46, 11 May - 09:15, 5 Jun 71	26	Incubation
	09:16, 5 Jun - 23:59, 30 Jun 71	26	Post-incubation
1695	00:00, 15 Apr - 09:16, 20 May 71	36	Pre-incubation
	09:17, 20 May - 11:36, 13 Jun 71	25	Incubation
	11:37, 13 Jun - 23:59, 21 Jun 71	9	Post-incubation
1698	06:46, 2 Jun - 23:59, 30 Jun 71	29	Post-incubation
1699	14:30, 30 May - 23:59, 6 Jun 71	8	Post-incubation
2200	15:01, 1 Jun - 23:59, 30 Jun 71	30	Post-incubation
2201	00:00, 2 Jun - 23:59, 30 Jun 71	29	Post-incubation
2202	13:20, 13 Jun - 23:59, 30 Jun 71	18	Post-incubation
2210	00:15, 1 Apr - 11:00, 15 May 72	45	Pre-incubation
	11:01, 15 May - 08:33, 24 May 72	10	Incubation
2219	06:00, 14 May - 03:59, 2 Jun 72	21	Incubation
2235	04:42, 13 May - 06:45, 6 Jun 72	25	Incubation
2238	09:02, 1 Apr - 20:00, 16 May 72	46	Pre-incubation
	20:01, 16 May - 14:05, 10 Jun 72	26	Incubation
2239	05:45, 1 Apr - 13:34, 13 May 72	43	Pre-incubation
	13:35, 13 May - 10:59, 7 Jun 72	26	Incubation
	11:00, 7 Jun - 10:00, 6 Jul 72	30	Post-incubation
2241	00:01, 4 Apr - 06:30, 10 May 72	37	Pre-incubation
	06:31, 10 May - 03:37, 26 May 72	17	Incubation
	03:38, 26 May - 23:59, 7 Jul 72	43	Post-incubation

Table 4. Data periods for analysis of activity. (continued)

Bird No.	Inclusive Dates	No. Days	Time Period
2246	00:01, 9 Apr - 05:00, 14 May 72	36	Pre-incubation
	05:01, 14 May - 10:37, 8 Jun 72	26	Incubation
	10:38, 8 Jun - 23:59, 25 Jun 72	18	Post-incubation
2248	05:16, 19 May - 08:25, 12 Jun 72	25	Incubation

Table 5. Percentage of time female grouse were active.

Bird No.	Pre-Incubation	Incubation	Post-Incubation	
			W/Brood	W/O Brood
1657	44.48	4.47	52.67	-
1690	51.21	4.82	-	-
1691	47.32	3.51	51.55	-
1695	48.68	3.91	58.38	-
1698	-	-	-	67.48
1699	-	-	56.94	-
2200	-	-	58.49	-
2201	-	-	-	60.54
2202	-	-	-	51.00
2210	47.91	4.95	-	-
2219	-	4.09	-	-
2235	-	3.11	-	-
2238	37.26	4.40	-	-
2239	55.56	5.84	54.39	-
2241	41.73	4.07	-	59.03
2246	48.38	3.45	47.09	-
2248	-	4.71	-	-
Mean:	46.95	4.28	54.22	59.51

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Figure 1a. Temporal distribution of percentage of 15-minute intervals active during the pre-incubation period for Hens 1657, 1690, and 1691.

NO. 1657

NO. 1690

NO. 1691

Figure 1b. Temporal distribution of percentage of
15-minute intervals active during the
pre-incubation period for Hens 1695, 2210,
and 2238.

NO. 1695

NO. 2210

NO. 2238

Figure 1c. Temporal distribution of percentage of 15-minute intervals active during the pre-incubation period for Hens 2239, 2241, and 2246.

NO. 2239

NO. 2241

NO. 2246

for several grouse of both sexes during November.

Activity levels tended to fluctuate during the day, but in most cases seldom fell below the 50% level. In several instances daytime levels of activity exceeded the dawn-dusk peaks.

Egg Laying

Figure 2 illustrates the daily periods of activity during the pre-incubation period for 2 hens from which nearly continuous data were obtained. Also illustrated are the times these birds were known to be at or near the nest site. It was assumed that eggs were laid during some of these visits to the nest, although it could not be determined exactly when egg laying occurred.

Visits to the nest site followed a definite pattern. Hens seldom visited the nest prior to the onset of egg-laying. During visits they usually remained inactive on the nest for one to several hours. Hens on the nest showed a tendency to remain inactive for longer periods as the clutch approached completion. A similar behavior was noted in the Spruce Grouse (Canachites canadensis franklinii) by McCourt et al. (1973).

Egg-laying visits occurred 1-5 days in succession at intervals ranging from 25 to 30 hours. Eggs were laid slightly later during each day of a laying sequence. When the next egg of a sequence was due sometime after the end of evening activity, the egg was not laid until the following morning. Thereafter, another sequence was begun with the usual 25-30 hour interval between

Figure 2. Daily periods of activity, visits to the nest site, and probable egg-laying periods for Hens 2241 and 2246 during the pre-incubation period. (___ = inactive, ... = active, --- = hen at or near nest site, * = nest visits during which egg-laying probably occurred, blank = no data.)

NO. 2241

NO. 2246

eggs. The number of days in a laying sequence varied among birds, and for the same individual as well. As examples, the laying sequences for several hens were the following: Hen 2210, 1-2-2-3-4; Hen 2239, 2-3-3-3; Hen 2241, 3-2-4-4; Hen 2246, 1-3-5-4. Numbers indicate the number of consecutive days during which egg-laying occurred while dashes indicate the skipping of a day between laying sequences. Similar patterns of egg-laying were observed for all hens monitored.

Egg-laying patterns similar to those of the present study have been found in domestic chickens (Gallus gallus) by Warren and Scott (1935), Scott and Warren (1936), and Heywang (1938), and Pheasants (Phasianus colchicus) by Labisky and Jackson (1966). Heywang (1938) found that the time interval between eggs decreased as the number of days in a laying sequence increased. Warren and Scott (1935) stated that differences in time intervals between eggs in a sequence were probably due to differences in the time an egg spends in the uterus. Scott and Warren (1936) determined that skipping of one or more days between laying sequences was caused by a delay in ovulation of the first egg of a sequence rather than the hen retaining a fully developed egg in the uterus.

Hen 1695, which had only 8 eggs and did not begin incubating until May 20, was believed to have renested. Figure 3 illustrates the activity periods of this hen during the pre-incubation period. Although some gaps occur in these data, the probable laying times of 7 eggs were determined. The remaining egg may have been laid during the data gap on the morning of 17 May. The first egg of

Figure 3. Daily periods of activity, visits to the nest site, probable egg-laying periods, and probable visits to a previous nest site for Hen 1695 during the pre-incubation period. (___ = inactive, ... = active, --- = hen at or near nest site, * = nest visits during which egg-laying probably occurred, ~ = hen at or near probable first nest site, blank = no data.)

NO. 1695

the clutch was laid on 9 May. Prior to this date a pattern of activity similar to that occurring during egg-laying was apparent. Inactive periods possibly associated with egg-laying are indicated in the figure. The film record indicates that these were all at a single location, approximately 160 yards from the nest. This suggests that an earlier nest had been established on 25 April, and that up to 10 eggs had been laid before they were likely destroyed by a predator on 8 May prior to the onset of incubation. The second nest was apparently established the following day on 9 May.

Incubation

Activity during incubation (Figure 4a, b, c) was limited to a few (usually 2-4) short feeding periods away from the nest each day. Kupa (1966), Schladweiler (1968), and Bump et al. (1947) reported similar findings for incubating Ruffed Grouse. However, temporal distribution of activity during the entire incubation period was not well documented by these workers. Kupa (1966) studied 4 nests for periods of 4 1/2 - 14 1/2 days and reported that most of 94 recorded absences of the hen occurred before 10:00 A.M. and after 5:00 P.M.

At Cedar Creek a shift in the temporal distribution of the first activity period of the day was apparent for all surviving hens as incubation progressed. Activity usually began prior to sunrise during the early stages of incubation, but later was delayed up to 4-5 hours after sunrise. The beginning of this

Figure 4a. Daily periods of activity during the incubation period for Hens 1690, 1691, and 1695. (___ = inactive, ... = active, --- = known disturbance by humans, blank = no data.)

NO. 1690

NO. 1691

NO. 1695

Figure 4b. Daily periods of activity during the incubation period for Hens 2235, 2238, and 2239. (___ = inactive, ... = active, --- = known disturbance by humans, blank = no data.)

NO. 2235

NO. 2238

NO. 2239

Figure 4c. Daily periods of activity during the
incubation period for Hens 2241, 2246,
and 2248. (___ = inactive, ... = active,
--- = known disturbance by humans, blank
= no data.)

NO. 2241

NO. 2246

NO. 2248

shift in activity ranged from 20-30 May in 1971, and from 16-25 May in 1972. Synchrony among hens was evident in 1972 when 5 of 7 hens began this shift during May 22-25. The shift occurred during different stages of the incubation period, i.e. from the fourth to the nineteenth day, for different hens. Weather data for both years beginning 5 days before the first hen began the activity shift, and ending 5 days after the last had begun the shift, are summarized in Table 6. No relationship was apparent between the onset of the activity shift and the average hourly temperature, wind velocity and direction, or precipitation.

A relationship between plant phenology and the activity shift was noted in 1972 when phenologic events were studied in detail. During the week of May 18-25 the leaves of most trees and shrubs reached full size. The rapid leafing out resulted in a "closing in" of the forest canopy. During this period the ferns which made up much of the understory grew rapidly and nearly reached full size. The net effect of this rapid leafing out was a marked reduction in the amount of light reaching the forest floor. Synchronization of circadian activity rhythms has been shown to be strongly affected by the day-night cycle of illumination (Aschoff, 1966). If the onset of activity during incubation is associated with light intensity at the nest, the activity would likely start later and later in the morning as the tree canopy leafed over and herbaceous vegetation grew up around the nest.

Table 6: Summary of weather data.

Date	Average Hourly Temperature	Wind		Precipitation	
		Total Mi./Day	Dominant Direction	Amount (Inches)	Approximate Time of Occurrence
May 15,71	61.5	106	WSW	0	
16	60.6	61	WSW	0	
17	61.2	80	SE	.30	05:00-07:00
18	48.9	163	N	0	
19	36.7	-	-	.90	00:00-18:00
20*	48.6	108	W	0	
21	51.2	78	ENE	0	
22	54.1	127	ESE	0	
23	53.6	100	E	1.02	07:00-24:00
24	49.0	97	W	.02	00:00-06:00
25*	44.1	147	W	.06	00:00-15:00
26	48.8	88	W	0	
27*	53.0	32	N	0	
28	57.4	65	SE	0	
29	63.5	83	SSW	0	
30*	58.7	-	-	0	
31	57.3	-	-	.05	05:00-09:00
June 1	53.4	-	NNW	.15	13:00-19:00
2	58.8	45	W	0	
3	66.4	40	SSW	0	
4	71.8	85	ESE	.05	19:00-24:00
May 11,72	54.8	78	ESE	0	
12	63.5	138	ESE	0	
13	52.9	108	NE	.15	06:30-10:00
14	51.9	108	NNW	0	
15	55.6	34	V	0	
16*	66.2	45	ESE	0	
17	71.3	56	SE	0	
18	70.7	59	SE	0	
19*	69.9	62	SSE	0	
20	69.4	50	S	T	06:00-09:30
21	65.9	39	NNE	.25	10:20-13:40
22*	69.5	107	ESE	0	
23*	66.3	54	V	.05	06:00-08:00
24	63.3	56	E	.25	17:00-20:30
25*	65.1	56	ESE	.03	18:00-20:00
26	66.7	54	ESE	0	
27	66.5	39	WSW	0	
28	63.0	14	V	.05	08:20-11:30
29	52.8	118	N	.30	05:30-06:20
30	48.0	134	NNE	0	

* Date on which one or more hens began activity shift.

Post-Incubation

Temporal distribution of percentage of 15 minute intervals active during the post-incubation period are illustrated in Figures 5a, b, and 6. With but a single exception (Hen 2202), once activity began in the morning the birds maintained a high percentage of activity throughout most of the daylight hours until activity ceased in the evening. These mid-day levels of activity tended to be higher than those observed during the pre-incubation period. A tendency for evening activity peaks to be greater than early morning peaks was evident during this period, but the pattern was not so consistent as it was during the pre-incubation period.

A difference in times of onset and cessation of activity between hens with broods and those without broods was readily apparent. Hens with broods did not attain the morning activity peak until 1 - 2-3/4 hours after sunrise. The evening peak was 15 minutes to 2 hours prior to sunset. Those without broods reached morning activity peaks 15-30 minutes after sunrise and evening peaks from 15 minutes before to 15 minutes after sunset.

Daily activity during the post-incubation period is shown for Hen 2239 (brood) and Hen 2241 (no brood) in Figure 7. Hen 2239 began activity 2-3 hours after sunrise during the first few days following hatching of the chicks. Thereafter the onset of activity became progressively earlier until it approached sunrise on the 13th day. For the first few days activity ceased in the evening about 45 minutes prior to sunset and then gradually

Figure 5a. Temporal distribution of percentage of 15-minute intervals active during the post-incubation period for Hens 1657, 1691, and 1695 (with broods).

NO. 1657

NO. 1691

NO. 1695

Figure 5b. Temporal distribution of percentage of
15-minute intervals active during the
post-incubation period for Hens 2200, 2239,
and 2246 (with broods).

Figure 6. Temporal distribution of percentage of
15-minute intervals active during the
post-incubation period for Hens 1698, 2201,
2202, and 2241 (without broods).

Figure 7. Daily periods of activity during the post-incubation period for Hen 2239 (brood) and Hen 2241 (no brood). (- = inactive, ... = active, blank spaces = no data).

NO. 2239

NO. 2241

approached sunset on 5 July. All hens with broods exhibited similar behavior with respect to morning and evening activity patterns.

On the other hand, Hen 2241 maintained a relatively constant pattern of beginning activity at or slightly before sunrise and ceasing activity at or slightly after sunset each day.

No doubt the delaying or morning activity onset and early evening activity cessation by brood hens is related to brooding of the chicks during the cooler periods of the day. Brooding is most pronounced during the first few days when the chicks are least able to maintain body temperatures. As the chicks grow older and more independent of the brooding hen, the activity periods of these hens gradually resemble those of broodless females.

Home Range

Data periods for analysis of home range are indicated in Table 7. Each time period represents a similar stage of the breeding cycle for all hens included, but does not necessarily include the same calendar dates for each bird.

Home range data for all birds are summarized in Table 8. Range size was determined by both the grid-square and minimum-area methods. Only the grid-square method was used during subsequent determinations of cumulative home range and habitat usage, since it more accurately reflected the area used by the birds. The maximum number of possible fixes per bird each day was 96, a

Table 7. Data periods for analysis of home range.

Bird No.	Pre-egg-laying	Egg-laying	Incubation
1657	00:00, 11 Apr-23:59, 23 Apr 71	00:00, 24 Apr-09:49, 8 May 71	09:50, 8 May-08:45, 3 Jun 71
1690	00:00, 7 Apr-23:59, 27 Apr 71	00:00, 28 Apr-09:39, 12 May 71	09:40, 12 May-10:15, 5 Jun 71
1691	00:00, 7 Apr-23:59, 22 Apr 71	00:00, 23 Apr-10:45, 11 May 71	10:46, 11 May-09:15, 5 Jun 71
1695	00:00, 15 Apr-23:59, 24 Apr 71	00:00, 25 Apr-09:16, 20 May 71	09:17, 20 May-11:36, 13 Jun 71
2210	00:00, 1 Apr-23:59, 28 Apr 72	00:00, 29 Apr-11:00, 15 May 72	11:01, 15 May-08:33, 24 May 72
2219	00:00, 1 Apr-23:59, 30 Apr 72	00:00, 1 May-05:59, 14 May 72	06:00, 14 May-03:59, 2 Jun 72
2235	-	-	04:42, 13 May-06:45, 6 Jun 72
2239	00:00, 1 Apr-23:59, 29 Apr 72	00:00, 30 Apr-13:34, 13 May 72	13:35, 13 May-10:59, 7 Jun 72
2241	00:05, 4 Apr-23:59, 23 Apr 72	00:00, 24 Apr-06:30, 10 May 72	06:31, 10 May-03:37, 26 May 72
2246	00:00, 9 Apr-23:59, 27 Apr 72	00:00, 28 Apr-05:00, 14 May 72	05:01, 14 May-10:37, 8 Jun 72

Table 7. Data periods for analysis of home range. (continued)

Bird No.	Post-incubation (Weeks)		
	First	Second	Third
1657	08:46, 3 Jun-23:59, 9 Jun 71	-	-
1691	09:16, 5 Jun-23:59, 11 Jun 71	00:00, 12 Jun-23:59, 18 Jun 71	00:00, 19 Jun-23:59, 25 Jun 71
1695	11:37, 13 Jun-23:59, 19 Jun 71	-	-
1698	06:46, 2 Jun-23:59, 8 Jun 71	00:00, 9 Jun-23:59, 15 Jun 71	00:00, 16 Jun-23:59, 22 Jun 71
1699	14:30, 30 May-23:59, 6 Jun 71	-	-
2200	15:01, 1 Jun-23:59, 8 Jun 71	00:00, 9 Jun-23:59, 15 Jun 71	00:00, 16 Jun-23:59, 22 Jun 71
2201	00:00, 2 Jun-23:59, 8 Jun 71	00:00, 9 Jun-23:59, 15 Jun 71	00:00, 16 Jun-23:59, 22 Jun 71
2202	13:20, 13 Jun-23:59, 20 Jun 71	00:00, 21 Jun-23:59, 27 Jun 71	-
2219	04:00, 2 Jun-23:59, 8 Jun 72	00:00, 9 Jun-23:59, 15 Jun 72	00:00, 16 Jun-23:59, 22 Jun 72
2235	06:46, 6 Jun-23:59, 12 Jun 72	00:00, 13 Jun-23:59, 19 Jun 72	00:00, 20 Jun-23:59, 26 Jun 72
2239	11:00, 7 Jun-23:59, 13 Jun 72	00:00, 14 Jun-23:59, 20 Jun 72	00:00, 21 Jun-23:59, 27 Jun 72
2241	03:38, 26 May-23:59, 1 Jun 72	00:00, 2 Jun-23:59, 8 Jun 72	00:00, 9 Jun-23:59, 15 Jun 72
2246	10:38, 8 Jun-23:59, 14 Jun 72	00:00, 15 Jun-23:59, 21 Jun 72	-

Table 7. Data periods for analysis of home range. (continued)

Bird No.	Post-incubation (Weeks)		
	Fourth	Fifth	Sixth
1657	-	-	-
1691	00:00, 26 Jun-23:59, 30 Jun 71	-	-
1695	-	-	-
1698	00:00, 23 Jun-23:59, 29 Jun 71	-	-
1699	-	-	-
2200	00:00, 23 Jun-23:59, 29 Jun 71	-	-
2201	00:00, 23 Jun-23:59, 29 Jun 71	-	-
2202	-	-	-
2219	00:00, 23 Jun-23:59, 29 Jun 72	00:00, 30 Jun-23:59, 6 Jul 72	-
2235	00:00, 27 Jun-23:59, 3 Jul 72	-	-
2239	00:00, 28 Jun-23:59, 4 Jul 72	-	-
2241	00:00, 16 Jun-23:59, 22 Jun 72	00:00, 23 Jun-23:59, 29 Jun 72	00:00, 30 Jun-23:59, 6 Jul 72
2246	-	-	-

Table 8. Home range data.

Bird No.	Time Period	No. of Days	No. of Fixes	Home Range (Acres)	Minimum Area Home Range (Acres)	Cumulative Home Range (Acres)	Post-Incubation Cumulative Home Range (Acres)
1657	Pre-Egg-Laying	13	308	23.38	78.73	23.38	-
	Egg-Laying	15	615	17.28	27.31	25.77	-
	Incubation	27	1797	2.22	2.81	25.86	-
	1st Week	7	245	14.23	22.90	33.96	14.23
1690	Pre-Egg-Laying	21	865	17.93	37.47	17.93	-
	Egg-Laying	15	511	10.07	14.08	22.44	-
	Incubation	25	1618	1.02	0.70	22.44	-
1691	Pre-Egg-Laying	16	753	14.23	15.18	14.23	-
	Egg-Laying	19	853	15.80	18.37	17.91	-
	Incubation	26	1620	3.42	4.59	18.00	-
	1st Week	7	412	9.52	12.34	20.48	9.52
	2nd Week	7	528	11.55	15.03	24.44	18.26
	3rd Week	7	463	8.78	9.44	27.11	21.20
	4th Week	5	296	8.41	8.59	28.03	22.12
1695	Pre-Egg-Laying	10	473	29.35	42.54	29.35	-
	Egg-Laying	26	1309	24.41	55.95	35.24	-
	Incubation	25	1719	3.79	10.92	35.61	-
	1st Week	7	324	16.54	26.67	37.27	-

Table 8. Home range data. (continued)

Bird No.	Time Period	No. of Days	No. of Fixes	Home Range (Acres)	Minimum Area Home Range (Acres)	Cumulative Home Range (Acres)	Post-Incubation Cumulative Home Range (Acres)
1698	1st Week	7	405	7.39	7.97	-	7.39
	2nd Week	7	365	4.53	4.23	-	8.95
	3rd Week	7	350	10.72	20.74	-	16.03
	4th Week	7	174	4.90	4.96	-	17.41
1699	1st Week	7	419	11.28	39.58	-	-
2200	1st Week	7	370	19.78	30.37	-	19.78
	2nd Week	7	350	20.80	42.62	-	28.52
	3rd Week	7	476	23.94	39.17	-	38.73
	4th Week	7	449	15.90	25.51	-	39.47
2201	1st Week	7	464	8.96	11.81	-	8.96
	2nd Week	7	360	5.45	5.40	-	10.80
	3rd Week	7	396	6.38	-	-	11.44
	4th Week	7	323	4.71	4.40	-	11.81
2202	1st Week	7	302	13.03	30.55	-	13.03
	2nd Week	7	420	5.08	4.55	-	13.95
2210	Pre-Egg-Laying	28	2001	39.74	95.77	39.74	-
	Egg-Laying	17	1128	34.56	59.88	50.96	-
	Incubation	10	602	1.48	1.07	50.96	-

Table 8. Home range data. (continued)

Bird No.	Time Period	No. of Days	No. of Fixes	Home Range (Acres)	Minimum Area Home Range (Acres)	Cumulative Home Range (Acres)	Post-Incubation Cumulative Home Range (Acres)
2219	Pre-Egg-Laying	30	2033	43.25	53.64	43.25	-
	Egg-Laying	14	926	22.27	25.76	45.55	-
	Incubation	20	503	0.83	0.37	45.55	-
	1st Week	7	407	14.42	27.81	49.14	14.42
	2nd Week	7	315	7.21	9.96	52.73	18.93
	3rd Week	7	373	7.21	14.18	53.93	21.14
	4th Week	7	260	4.90	4.84	55.22	22.89
	5th Week	7	194	3.88	3.45	55.59	23.26
2235	Incubation	25	1030	2.50	2.80	2.50	-
	1st Week	7	255	10.17	37.93	-	10.17
	2nd Week	7	285	20.98	29.71	-	25.99
	3rd Week	7	246	20.79	46.36	-	38.32
	4th Week	7	266	19.22	42.37	-	42.37
2239	Pre-Egg-Laying	29	1672	56.56	183.57	56.56	-
	Egg-Laying	14	747	18.21	19.65	59.50	-
	Incubation	26	1304	3.05	2.40	59.50	-
	1st Week	7	288	11.83	17.82	61.25	11.83
	2nd Week	7	436	20.15	46.36	69.99	25.91
	3rd Week	7	391	26.25	60.54	84.43	41.83
	4th Week	7	371	18.12	37.12	96.67	56.09

Table 8. Home range data. (continued)

Bird No.	Time Period	No. of Days	No. of Fixes	Home Range (Acres)	Minimum Area Home Range (Acres)	Cumulative Home Range (Acres)	Post-Incubation Cumulative Home Range (Acres)
2241	Pre-Egg-Laying	20	1405	22.37	45.31	22.37	-
	Egg-Laying	17	1165	28.19	33.60	34.05	-
	Incubation	17	1322	1.57	1.15	34.05	-
	1st Week	7	493	11.09	20.65	38.01	11.09
	2nd Week	7	536	8.79	16.43	41.87	17.07
	3rd Week	7	404	14.53	52.26	45.73	22.68
	4th Week	7	466	19.50	37.26	55.94	37.22
	5th Week	7	469	12.20	14.25	56.77	41.54
	6th Week	7	442	13.49	16.65	56.86	43.84
2246	Pre-Egg-Laying	19	1370	21.26	39.50	21.26	-
	Egg-Laying	17	1349	15.62	34.04	25.86	-
	Incubation	26	1731	2.40	2.20	25.86	-
	1st Week	7	496	6.47	5.96	25.86	6.47
	2nd Week	7	540	24.59	51.89	35.24	24.78

figure not attained during the study. The mean percentage of this maximum for all birds during all time periods was 58.7%. Home range sizes between periods for an individual, or for similar periods for different individuals, are not directly comparable unless the periods were comprised of equal numbers of days, e.g., the 7-day periods after incubation. As shown by cumulative home ranges, the calculated home range of an individual increased in size as the number of days of data increased. However, data from the egg-laying period, which ranged from 14 to 19 days (excluding Hen 1695), may be compared among birds. This degree of variation in number of days probably had little effect on range sizes. Incubation data are also comparable among birds, since during this period hens evidently left the nest only to feed and often returned to the same feeding locations repeatedly. Thus, the home range for the incubation period was well delineated after only a few days.

Mean home range sizes for all periods except pre-egg-laying are presented in Table 9. The largest and smallest mean range sizes were found during the egg-laying and incubation periods respectively. Mean home range size for hens with broods was greater during all periods of comparison than mean range size of hens without broods.

Figure 8 illustrates the weekly post-incubation home range sizes for all birds. Home range sizes for hens with and without broods were similar during the first week after incubation. During the second week hens with broods increased their range

Table 9. Mean home range sizes (acres).

		Egg-Laying	Incubation	Post-Incubation				
				1st Week	2nd Week	3rd Week	4th Week	5th Week
All Birds	Mean	20.71	2.23					
	Range	10.07-34.56	0.83-3.79					
	Sample Size	9	10					
Hens w/ Broods	Mean			12.47	17.82	19.94	15.41	
	Range			6.47-19.78	8.87-24.59	8.78-26.25	8.41-19.22	
	Sample Size			8	6	4	4	
Hens w/o Broods	Mean			10.97	6.21	9.71	8.50	8.04
	Range			7.39-14.42	4.53-8.79	6.38-14.53	4.71-19.50	3.88-12.20
	Sample Size			5	5	4	4	2

size while those without broods decreased their range size. Home ranges for all birds except Hen 2241 decreased after the third week.

Cumulative home ranges (Figure 9) of hens with broods increased rapidly during the post-incubation period. These hens, which used larger areas each week than broodless hens, continually moved into new areas. The gradual increase in cumulative range size of hens without broods indicates that these birds were quite sedentary. They utilized primarily the same areas from one week to the next.

When home range maps for all hens during a given period were overlaid on the habitat map, relatively little overlap between birds was evident in most cases. This suggests that some spacing mechanism may be operating among females during this time. MacDonald (1970) stated that female Rock Ptarmigan (Lagopus mutus) and Franklin's race of the Spruce Grouse become aggressive toward other females of their respective species during the breeding season. Haas (1974) and Stirling (1968) noted that female Spruce Grouse and Blue Grouse (Dendragapus obscurus fuliginosus) respectively, became aggressive toward other hens especially during the egg-laying period. Aggressiveness among female Greater Prairie Chickens (Tympanuchus cupido pinnatus) on booming grounds was reported by Robel (1970).

There is some evidence that female Ruffed Grouse become aggressive toward other females in spring. Three captive female grouse (2 adults, 1 juvenile), which were held over winter in a

Figure 8. Weekly home range sizes during the post-incubation period for hens with and without broods.

HOME RANGE SIZE (Acres)

Figure 9. Cumulative home range size during the post-incubation period for hens with and without broods.

large enclosure, showed no notable animosity toward one another until the following spring. On 12 April, 1973 the juvenile was severely scalped with a large open wound exposing the base of the skull. On 6 April, 1971 Hens 1690 and 1691 were captured simultaneously in a lily-pad trap. The former had been slightly scalped by the time it was removed from the trap.

Under wild conditions injuries of this type probably seldom occur. Individuals being attacked simply fly away. Aggressive encounters between hens in the wild are probably brief and usually difficult to observe. Not all female grouse on the study area were radio-marked and whether female grouse were territorial during this period remains questionable. Some nests were located quite close to each other, e.g. Nos. 1690 and 2202 were 55 yards apart, and Nos. 2238 and 2248 only 39 yards apart. On several occasions unmarked broods were flushed within 50 yards of radio-marked broods. The question of spacing and aggressiveness between females during the breeding season requires further study.

Vegetation Analysis

A total of 63 habitat types were differentiated on the study area. After studying the habitat usage of the female grouse, it was apparent that these birds were not differentiating habitats in the same manner as humans. Thus, although 9 categories of alder swamp were described, use of any one by a hen seemed largely dependent upon which particular types were present within the area normally traversed by the bird. When more than one of

the 9 types was available to a bird, they were used interchangeably. The same could be said of other habitats. Since many of the habitat types described by man make up less than 1% of the study area, the 63 categories were lumped into 10 major habitat groups. These are described below. All scientific names are from Gleason and Cronquist (1963).

(1) Oak - An upland type composed largely of mature red oak (Quercus borealis) and northern pin oak (Q. ellipsoidalis) 25-60 feet high with scattered white birch (Betula papyrifera), big-tooth aspen (Populus grandidentata) and/or trembling aspen. The understory consists of sparse to dense hazel (Corylus sp.) with scattered ferns, grasses, sedges, wild geraniums (Geranium sp.) and large-leafed aster (Aster macrophyllus).

(2) White Birch - Largely mature white birch 25-60 feet high with scattered trembling aspen. The understory consists of scattered hazel and/or alder (Alnus rugosa) with dense lady ferns (Athyrium Felix-femina) and interrupted fern (Osmunda Claytoniana). This type is often found in the transition zone between upland and lowland habitats.

(3) Aspen - Mostly pole size to mature trembling aspen 15-60 feet high with a few clones of mature big-tooth aspen. The understory consists of hazel, alder, and/or dense lady fern, interrupted fern and sensitive fern (Onoclea sensibilis). This type is often found in the transition zone between upland and lowland types.

(4) Mixed Hardwoods - Composed of varying combinations of white birch, yellow birch (Betula lutea), trembling aspen, red maple (Acer rubrum), American elm (Ulmus americana), black ash (Fraxinus nigra), and tamarack (Larix laricina). The understory is composed of scattered alders and dogwoods (Cornus sp.), usually with dense ferns dominated by cinnamon fern (Osmunda cinnamomea), and lady fern. This type is usually somewhat hummocky and often has areas of standing water in spring.

(5) White Cedar--Largely mature white cedar (Thuja occidentalis) with scattered tamarack and/or white birch. This type often contains many deadfalls. There is little or no shrub understory present. The forest floor is covered largely by mosses and usually has pockets of standing water throughout the growing season.

(6) Tamarack - Consists largely of pole size to mature tamarack 15-75 feet high with scattered white cedar and/or white birch. The understory is usually sparse or moderately dense with alder, dogwood, and/or poison sumac (Rhus Vernix). The herbaceous layer is often dominated by cinnamon ferns. The ground is hummocky and usually has pockets of standing water throughout the growing season.

(7) Alder - Composed primarily of alder 6-15 feet high with varying combinations of dogwood, willow (Salix sp.) and poison sumac. It may contain scattered American elm, red maple, white birch, trembling aspen, or tamarack. The understory often consists of dense jewel weed (Impatiens biflora), as well as sedges,

ferns, nettles (Urtica sp.) and marsh marigolds (Caltha palustris). The ground is hummocky and usually wet throughout the growing season.

(8) Mixed Shrubs - Composed of varying combinations of willow, dogwood, bog birch (Betula pumila) and alder. This type sometimes contains scattered pole-size tamarack, white birch, or white cedar. The understory is usually dominated by sedges and grasses with scattered cattails (Typha latifolia). The ground is hummocky and normally wet throughout the growing season.

(9) Marsh - Usually dominated by grasses, sedges and/or cattails with scattered alder, bog birch, willow, or dogwood. The ground is normally wet throughout the growing season.

(10) Open Field - Mostly old fields not recently cultivated. Vegetation consists of various grasses, scattered mullein (Verbascum Thapsus), burr clover (Lespedeza capitata), etc.

Habitat usage by individual hens during the pre-egg-laying, egg-laying, and weekly intervals after incubation is summarized in Tables 10-20. Habitat usage during incubation will be discussed separately. Among individuals, habitat usage was quite variable during a given period and appeared to be a reflection of the distribution of habitat types on the study area. Although the various habitats occurred throughout the study area, the acreages of each were not evenly distributed. The relationship of usage to distribution is demonstrated for 2 hens during the egg-laying period. The area utilized by Hen 1657 (Table 11) was largely composed of tamarack and 51.71% of the fixes were in that

Table 10. Habitat usage by individual female grouse during the pre-egg-laying period.

Habitat Types	No. 1657		No. 1690		No. 1691	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	2.77	2.59	13.48	11.84	4.52	1.32
White Birch	-	-	1.04	0.24	-	-
Mixed Hardwoods	11.48	15.59	17.62	33.97	14.84	6.76
Aspen	3.56	0.65	8.81	18.66	18.07	8.35
White Cedar	4.35	3.90	29.53	22.24	-	-
Tamarack	57.70	63.31	10.35	3.95	7.10	1.60
Alder	10.27	7.79	9.33	6.10	36.12	72.94
Mixed Shrubs	3.16	2.60	2.07	0.84	0.64	0.80
Open Field	1.18	0.97	3.11	0.84	4.52	0.53
Marsh	5.53	2.60	4.66	1.32	14.19	7.70

Table 10. Habitat usage by individual female grouse during the pre-egg-laying period. (continued).

Habitat Types	No. 1695		No. 2210		No. 2219	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	6.07	3.44	14.11	7.77	22.43	7.61
White Birch	14.69	16.34	14.36	26.42	7.70	5.94
Mixed Hardwoods	32.59	37.84	16.44	13.93	14.74	27.90
Aspen	2.88	6.24	2.54	5.91	4.27	7.42
White Cedar	15.65	4.30	4.63	2.86	-	-
Tamarack	-	-	18.06	8.93	3.21	2.26
Alder	17.25	23.88	17.35	29.73	40.17	47.05
Mixed Shrubs	-	-	0.93	2.05	0.43	0.00
Open Field	8.63	4.52	9.26	2.10	0.43	0.20
Marsh	2.24	3.44	2.32	0.30	6.62	1.62

Table 10. Habitat usage by individual female grouse during the pre-egg-laying period. (continued)

Habitat Types	No. 2239		No. 2241		No. 2246	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	11.58	13.51	30.84	10.94	5.68	0.87
White Birch	4.08	12.56	12.91	11.00	12.67	3.19
Mixed Hardwoods	17.29	13.10	0.83	0.07	31.44	33.82
Aspen	1.95	5.74	5.00	3.57	3.93	7.67
White Cedar	20.89	15.55	2.92	0.21	20.52	29.04
Tamarack	9.95	1.90	3.75	4.57	0.87	0.14
Alder	17.78	32.67	36.67	65.57	11.35	15.21
Mixed Shrubs	6.04	2.87	-	-	-	-
Open Field	5.22	1.08	4.58	1.36	9.17	2.17
Marsh	5.22	1.02	2.50	2.71	4.37	7.89

Table 11. Habitat usage by individual female grouse during the egg-laying period.

Habitat Types	No. 1657		No. 1690		No. 1691	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	6.96	8.13	14.81	17.43	7.01	17.12
White Birch	-	-	-	-	-	-
Mixed Hardwoods	12.83	9.93	25.93	34.85	11.70	3.40
Aspen	1.07	1.30	12.96	21.59	19.88	19.93
White Cedar	4.28	4.55	12.03	15.25	-	-
Tamarack	54.54	51.71	1.85	0.40	-	-
Alder	13.90	17.23	9.26	6.73	42.11	56.28
Mixed Shrubs	3.21	5.20	-	-	1.17	0.35
Open Field	-	-	20.38	2.96	6.43	0.47
Marsh	3.21	1.95	2.78	0.79	11.70	2.45

Table 11. Habitat usage by individual female grouse during the egg-laying period. (continued)

Habitat Types	No. 1695		No. 2210		No. 2219	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	2.27	0.92	16.58	18.32	15.70	2.59
White Birch	27.65	37.67	4.28	1.33	14.46	15.56
Mixed Hardwoods	24.24	26.21	18.72	27.15	3.31	4.21
Aspen	2.28	4.01	3.74	6.14	7.02	1.62
White Cedar	9.85	5.70	4.01	1.96	-	-
Tamarack	-	-	22.99	11.56	4.55	4.32
Alder	22.35	21.95	15.78	22.60	45.86	67.38
Mixed Shrubs	1.51	0.46	-	-	-	-
Open Field	5.30	1.23	7.75	3.02	2.48	0.22
Marsh	4.55	1.85	6.15	7.92	6.62	4.10

Table 11. Habitat usage by individual female grouse during the egg-laying period. (continued)

Habitat Types	No. 2239		No. 2241		No. 2246	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	10.15	8.92	38.10	22.55	2.50	1.27
White Birch	4.57	2.66	7.28	10.32	18.75	1.71
Mixed Hardwoods	24.37	26.35	-	-	23.75	17.07
Aspen	1.01	0.40	7.61	7.24	10.00	16.32
White Cedar	13.20	3.33	-	-	13.13	7.60
Tamarack	2.03	0.27	4.30	1.08	-	-
Alder	31.99	42.36	34.76	57.82	6.25	37.55
Mixed Shrubs	10.65	15.58	2.32	0.00	-	-
Open Field	-	-	2.65	0.90	15.62	2.16
Marsh	2.03	0.13	2.98	0.09	10.00	16.32

Table 12. Habitat usage by hens with broods during the first week after hatching.

Habitat Types	No. 1657		No. 1691		No. 1695		No. 1699	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	-	-	10.68	12.89	7.82	5.23	18.85	8.91
White Birch	-	-	-	-	17.88	20.62	-	-
Mixed Hardwoods	22.73	30.61	24.27	20.68	35.76	35.38	29.51	51.35
Aspen	1.30	1.22	11.65	10.22	2.79	2.77	3.28	1.62
White Cedar	8.44	22.45	-	-	17.32	11.08	0.82	0.28
Tamarack	51.30	33.88	7.78	5.85	-	-	29.51	28.65
Alder	11.69	9.39	33.98	46.71	10.05	20.00	13.93	8.11
Mixed Shrubs	-	-	-	-	-	-	-	-
Open Field	-	-	4.85	0.73	8.38	4.92	4.10	1.08
Marsh	4.54	2.45	6.79	2.92	-	-	-	-

Table 12. Habitat usage by hens with broods during the first week after hatching. (continued)

Habitat Types	No. 2200		No. 2235		No. 2239		No. 2246	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	7.98	5.67	75.46	87.06	9.38	2.45	2.86	0.40
White Birch	16.91	31.35	7.27	7.85	1.56	1.05	7.14	3.02
Mixed Hardwoods	35.68	29.19	-	-	30.47	41.60	55.71	75.60
Aspen	1.88	2.16	3.64	0.78	3.12	1.05	7.15	1.21
White Cedar	12.68	3.52	-	-	3.91	0.35	8.57	2.02
Tamarack	-	-	0.91	0.39	3.12	1.75	-	-
Alder	10.79	20.00	3.63	3.14	38.29	47.55	11.42	14.52
Mixed Shrubs	-	-	-	-	9.37	4.20	-	-
Open Field	9.86	3.25	9.09	0.78	-	-	2.86	2.02
Marsh	4.22	4.86	-	-	0.78	0.00	4.29	1.21

Table 13. Habitat usage by hens with broods during the second week after hatching.

Habitat Types	No. 1657		No. 1691		No. 2200	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	14.58	6.75	-	-	2.67	2.01
White Birch	13.55	18.56	-	-	27.55	22.63
Mixed Hardwoods	39.58	55.69	11.20	10.06	26.21	32.95
Aspen	-	-	18.40	15.18	-	-
White Cedar	3.13	2.11	-	-	7.56	12.32
Tamarack	16.66	11.40	40.00	52.94	-	-
Alder	12.50	5.49	10.40	1.71	23.56	12.90
Mixed Shrubs	-	-	7.20	15.18	0.89	0.57
Open Field	-	-	1.60	0.95	6.67	3.44
Marsh	-	-	11.20	3.98	4.89	13.18

Table 13. Habitat usage by hens with broods during the second week after hatching. (continued)

Habitat Types	No. 2235		No. 2239		No. 2246	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	80.70	91.58	15.32	18.88	3.77	0.93
White Birch	7.02	1.75	12.16	28.21	18.11	25.28
Mixed Hardwoods	-	-	14.42	4.20	25.29	32.52
Aspen	-	-	-	-	4.90	3.35
White Cedar	-	-	4.50	4.89	7.55	10.04
Tamarack	7.46	3.86	6.76	5.12	3.77	6.88
Alder	-	-	28.38	32.64	15.09	9.11
Mixed Shrubs	-	-	8.55	3.50	1.13	0.56
Open Field	4.82	2.81	9.46	2.56	13.59	7.06
Marsh	-	-	0.45	0.00	6.80	4.27

Table 14. Habitat usage by hens with broods during the third week after hatching.

Habitat Types	No. 1691		No. 2200		No. 2235	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	-	-	5.79	8.40	54.23	61.07
White Birch	-	-	11.97	20.81	10.22	4.10
Mixed Hardwoods	4.21	0.86	27.41	24.15	-	-
Aspen	12.63	5.18	2.32	1.26	-	-
White Cedar	-	-	7.34	2.31	-	-
Tamarack	60.01	67.61	1.16	0.85	3.56	11.47
Alder	5.26	5.62	37.44	36.76	-	-
Mixed Shrubs	17.89	20.73	6.18	5.25	-	-
Open Field	-	-	0.39	0.21	28.44	22.95
Marsh	-	-	-	-	3.55	0.41

Table 14. Habitat usage by hens with broods during the third week after hatching. (continued)

HabitatTypes	No. 2239		No. 2246	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	26.96	37.26	2.23	1.67
White Birch	5.32	0.80	16.19	15.06
Mixed Hardwoods	11.34	27.06	29.06	25.11
Aspen	1.77	0.27	6.71	20.92
White Cedar	2.83	0.54	5.59	2.51
Tamarack	3.90	0.80	-	-
Alder	24.46	21.20	7.82	19.67
Mixed Shrubs	0.71	0.54	-	-
Open Field	8.16	4.83	25.14	10.46
Marsh	14.55	6.70	7.26	4.60

Table 15. Habitat usage by hens with broods during the fourth week after hatching.

Habitat Types	No. 1691		No. 2200		No. 2235		No. 2239	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	-	-	3.51	0.69	54.81	63.90	3.59	1.64
White Birch	-	-	25.74	33.19	5.77	4.51	28.20	49.99
Mixed Hardwoods	7.69	1.69	33.33	25.11	-	-	18.46	7.65
Aspen	13.19	7.43	-	-	-	-	1.02	2.18
White Cedar	-	-	10.53	13.13	-	-	5.64	2.46
Tamarack	71.43	78.38	-	-	12.02	7.15	-	-
Alder	-	-	16.95	26.50	0.48	13.16	5.13	22.68
Mixed Shrubs	7.69	12.50	-	-	-	-	-	-
Open Field	-	-	9.36	1.38	23.08	8.65	28.73	10.12
Marsh	-	-	0.58	0.00	3.84	2.63	9.23	3.28

Table 16. Habitat usage by broodless hens during the first week after nest destruction.

Habitat Types	No. 1698		No. 2201		No. 2202	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	17.72	3.21	-	-	5.00	5.00
White Birch	-	-	14.43	4.09	3.56	2.00
Mixed Hardwoods	-	-	-	-	13.57	8.67
Aspen	8.86	0.99	3.09	1.08	-	-
White Cedar	-	-	-	-	27.86	9.00
Tamarack	11.40	4.69	7.22	5.17	30.00	31.34
Alder	62.02	91.11	58.77	83.42	4.30	7.32
Mixed Shrubs	-	-	-	-	15.71	36.67
Open Field	-	-	1.03	0.21	-	-
Marsh	-	-	15.46	6.03	-	-

Table 16. Habitat usage by broodless hens during the first week after nest destruction. (continued)

Habitat Types	No. 2219		No. 2241	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	9.61	6.14	20.34	11.03
White Birch	6.41	6.39	16.10	11.62
Mixed Hardwoods	17.31	27.27	-	-
Aspen	1.28	0.98	11.02	4.90
White Cedar	-	-	-	-
Tamarack	1.92	1.23	-	-
Alder	60.27	56.76	38.97	53.88
Mixed Shrubs	-	-	-	-
Open Field	-	-	10.18	5.51
Marsh	3.20	1.23	3.39	13.06

Table 17. Habitat usage by broodless hens during the second week after nest destruction.

Habitat Types	No. 1698		No. 2201		No. 2202	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	-	-	6.78	0.55	-	-
White Birch	-	-	10.18	3.05	1.82	0.24
Mixed Hardwoods	-	-	-	-	-	-
Aspen	-	-	1.69	0.28	-	-
White Cedar	-	-	-	-	3.64	3.57
Tamarack	12.25	7.16	11.86	11.40	49.09	72.62
Alder	81.63	90.91	62.71	84.44	-	-
Mixed Shrubs	-	-	-	-	45.45	23.57
Open Field	-	-	-	-	-	-
Marsh	6.12	1.93	6.78	0.28	-	-

Table 17. Habitat usage by broodless hens during the second week after nest destruction.
(continued)

Habitat Types	No. 2219		No. 2241	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	1.30	0.32	14.73	29.15
White Birch	-	-	29.48	5.80
Mixed Hardwoods	27.28	7.62	7.37	6.92
Aspen	5.19	3.81	1.05	1.68
White Cedar	-	-	6.32	0.19
Tamarack	-	-	-	-
Alder	66.23	88.25	23.16	51.78
Mixed Shrubs	-	-	-	-
Open Field	-	-	17.89	4.48
Marsh	-	-	-	-

Table 18. Habitat usage by broodless hens during the third week after nest destruction.

Habitat Types	No. 1698		No. 2201		No. 2219		No. 2241	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	5.22	12.58	4.35	0.50	3.85	1.88	5.76	3.52
White Birch	1.74	0.00	18.84	5.81	-	-	25.01	23.55
Mixed Hardwoods	7.83	3.14	-	-	30.77	19.57	13.46	6.02
Aspen	2.61	0.57	2.90	0.50	2.56	1.34	5.76	20.80
White Cedar	-	-	-	-	-	-	3.85	1.00
Tamarack	7.82	16.00	11.59	4.55	-	-	-	-
Alder	55.65	48.86	55.07	86.62	60.26	68.63	30.78	35.09
Mixed Shrubs	14.78	15.71	-	-	-	-	-	-
Open Field	-	-	-	-	-	-	14.10	9.77
Marsh	4.35	3.14	7.25	2.02	2.56	8.58	1.28	0.25

Table 19. Habitat usage by broodless hens during the fourth week after nest destruction.

Habitat Types	No. 1698		No. 2201		No. 2219		No. 2241	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	7.55	1.15	-	-	3.70	0.38	6.73	2.38
White Birch	3.77	0.57	8.00	2.17	-	-	3.85	0.65
Mixed Hardwoods	-	-	-	-	11.11	1.92	13.47	4.75
Aspen	7.55	2.30	-	-	11.11	3.08	1.92	0.43
White Cedar	-	-	-	-	-	-	1.44	0.65
Tamarack	11.32	31.04	12.00	11.15	-	-	6.73	3.67
Alder	37.74	41.95	70.00	82.97	74.08	94.62	47.59	79.69
Mixed Shrubs	32.07	22.99	-	-	-	-	-	-
Open Field	-	-	-	-	-	-	-	-
Marsh	-	-	10.00	3.71	-	-	18.27	7.78

Table 20. Habitat usage by broodless hens during the fifth week after nest destruction.

Habitat Types	No. 2219		No. 2241	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	-	-	9.92	2.98
White Birch	-	-	9.16	17.48
Mixed Hardwoods	-	-	-	-
Aspen	9.52	3.09	0.76	0.00
White Cedar	-	-	-	-
Tamarack	-	-	10.69	21.75
Alder	90.48	96.91	63.36	56.30
Mixed Shrubs	-	-	-	-
Open Field	-	-	-	-
Marsh	-	-	6.11	1.49

type. In contrast, very little tamarack was present in the area occupied by Hen 1690 and only 0.40% of the fixes fell in that habitat. Most differences in individual habitat usage during a given period can be explained in this manner.

In order to obtain a clearer picture of habitat usage by female grouse within the defined area, mean values were calculated of both the percentage of grid squares and percentage of fixes within a bird's home range that fell within each habitat type (Tables 21-23).

To ascertain whether female grouse are selecting or avoiding certain habitats, the availability of habitats to the birds must first be determined. In similar analyses of habitat usage, Berg (1970) and Nicholls and Warner (1972) considered that the habitats available to moose and barred owl, respectively were those habitat types within an individual's home range. This method does not seem entirely satisfactory in the case of grouse. If an animal is selecting habitats, the habitats within its home range reflect that choice. If social and/or behavioral factors such as territoriality are not restricting the movements of an animal, habitats falling outside an individual's home range would have to be considered available to that animal if it chose to use them. For example, the home ranges of several Cedar Creek hens bordered open fields, but this kind of habitat was seldom utilized by these birds, though obviously available to them. It would be incorrect to say that only the habitats within the home range of a grouse hen were available to it, and also incorrect to

Table 21. Mean habitat usage by grouse hens during the pre-egg-laying and egg-laying periods.

Habitat Types	Occurrence On Study Area (%)	Pre-Egg-Laying		Egg-Laying	
		Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	22.92	12.39	6.65	12.68	10.80
White Birch	2.46	7.49	8.41	8.55	7.70
Mixed Hardwoods	10.42	17.48	20.33	16.10	16.58
Aspen	3.50	5.68	7.13	7.28	8.74
White Cedar	6.14	10.94	8.68	6.28	4.26
Tamarack	9.74	12.33	9.63	10.03	7.70
Alder	15.82	21.81	33.44	24.69	36.65
Mixed Shrubs	5.23	1.47	1.02	2.10	2.40
Open Field	14.00	5.12	1.53	6.73	1.22
Marsh	9.86	5.29	3.18	5.56	3.95

Table 22. Mean habitat usage by hens with broods.

Habitat Types	Occurrence On Study Area (%)	Weeks After Hatching							
		First		Second		Third		Fourth	
		Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	22.92	16.63	15.33	19.52	20.02	17.84	21.68	15.48	16.56
White Birch	2.46	6.34	7.99	13.06	16.07	8.74	8.15	14.93	21.92
Mixed Hardwoods	10.42	29.27	35.55	19.45	22.57	14.40	15.44	14.88	8.62
Aspen	3.50	4.35	2.63	3.88	3.09	4.69	5.53	3.55	2.40
White Cedar	6.14	6.47	4.96	3.79	4.89	3.15	1.07	4.04	3.90
Tamarack	9.74	11.58	8.81	12.44	13.37	13.73	16.15	20.86	21.38
Alder	15.82	16.72	21.18	14.99	10.31	15.00	16.65	5.64	15.58
Mixed Shrubs	5.23	1.17	0.52	2.96	3.30	4.96	5.30	1.92	3.12
Open Field	14.00	4.89	1.60	6.02	2.80	12.42	7.69	15.29	5.04
Marsh	9.86	2.58	1.43	3.89	3.58	5.07	2.34	3.41	1.48

Table 23. Mean habitat usage by hens without broods.

Habitat Types	Occurrence On Study Area (%)	Weeks After Nest Destruction					
		First		Second		Third	
		Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	22.92	10.53	5.08	4.56	6.00	4.80	4.62
White Birch	2.46	8.10	4.82	8.30	1.82	11.40	7.34
Mixed Hardwoods	10.42	6.18	7.19	6.93	2.91	13.01	7.18
Aspen	3.50	4.85	1.59	1.59	1.15	3.46	5.80
White Cedar	6.14	5.57	1.80	1.99	0.75	0.96	0.25
Tamarack	9.74	10.11	8.49	14.64	18.24	4.85	5.14
Alder	15.82	44.87	58.50	46.74	63.08	50.44	59.80
Mixed Shrubs	5.23	3.14	7.33	9.09	4.71	3.70	3.93
Open Field	14.00	2.24	1.14	3.58	0.90	3.52	2.44
Marsh	9.86	4.41	4.06	2.58	0.44	3.86	3.50

Table 23. Mean habitat usage by hens without broods. (continued)

Habitat Types	Weeks After Nest Destruction			
	Fourth		Fifth	
	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)	Grid Sq. In Each Habitat (%)	Fixes In Each Habitat (%)
Oak	4.49	0.98	4.96	1.49
White Birch	3.90	0.85	4.58	8.74
Mixed Hardwoods	6.15	1.67	0.00	0.00
Aspen	5.15	1.45	5.15	1.55
White Cedar	0.36	0.16	0.00	0.00
Tamarack	7.51	11.46	5.34	10.87
Alder	57.35	74.81	76.92	76.60
Mixed Shrubs	8.02	5.75	0.00	0.00
Open Field	0.00	0.00	0.00	0.00
Marsh	7.07	2.87	3.05	0.75

say that every portion of the defined study area was available to a given bird. The home range analysis in the present study showed that each radio-marked hen used only a small portion of the defined area. When all home range maps were overlaid on the vegetation map simultaneously, it was readily apparent that almost the entire defined area was used at some time by one or more birds. In effect, the entire area could be considered available to the radio-marked female grouse population. It then follows that the mean values for habitat usage (Tables 21-23) for each time period are comparable with the occurrence of habitat types on the defined area to determine preferences or avoidances of those habitats.

Chi square tests using mean values were conducted for each time period. The formula utilized was the following;

$$\chi^2 = \bar{N} \sum_{i=1}^K \frac{(\hat{P}_i - P_i)^2}{P_i}$$

where $\bar{N}$ = the mean number of fixes for all birds during a given time period; $\hat{P}_i$ = the mean fraction of fixes observed in the i th habitat type; P_i = the fraction of the defined study area comprised of the i th habitat type. The null hypothesis was the following: if female grouse entered different habitat types by chance alone, the mean number of fixes falling in each habitat type should be proportional to the occurrence of the habitat types on the defined study area. For all time periods the null hypothesis was rejected at the 0.005 level indicating that these birds were exhibiting significant preferences or avoidances of given habitat types.

Preferences or avoidances of each habitat type over time, and differences between hens with and without broods, are illustrated in Figure 10. The plotted values were obtained by subtracting the percentage occurrence of a given habitat on the defined area from the mean percentage of fixes falling in that habitat type (Tables 21-23). A positive value indicates preferential use of that habitat. As this value increases, stronger preferences for that type are indicated. Negative values indicate avoidance of that habitat. The minimum negative value can be no lower than the percentage availability of the habitat on the study area, i.e. zero usage of the white birch type would be recorded as only a -2.46 on the graph, since white birch makes up only 2.46% of the study area.

Figure 10 indicates alder habitats were preferred prior to incubation. After incubation preferential use of alder by hens without broods increased markedly. Hens with broods utilized alder in proportion to its availability.

Mixed hardwoods were preferred prior to incubation, but these tended to be avoided by hens without broods. Hens with broods exhibited a strong preference for hardwoods during the first week after hatching, but use of these dropped off in an almost linear manner until they were avoided during the fourth week.

With respect to tamarack, a nearly opposite trend occurred. Tamarack use by hens with broods increased in an almost linear manner over the 4 week period. Usage of tamarack by hens without broods did not indicate consistent preferences or avoidances.

Figure 10. Preference or avoidance of habitat types by female grouse during pre-egg-laying, egg-laying, and weekly intervals after incubation. (+ = preference, - = avoidance, --- = all birds, ... = hens with broods, ____ = hens without broods.)

White birch and aspen types were preferred prior to incubation. After incubation, birch received preferential use by hens with broods while aspen was used in close proportion to its availability.

Although oak types generally were avoided, they received their greatest usage by hens with broods. This usage was primarily by Hen 2235 which utilized an atypical oak type in that the understory was dominated by dense stands of raspberries (Rubus sp.)

No pronounced preferences or avoidances of the mixed shrub type were indicated.

Open field, marsh, and cedar swamp were mostly avoided.

Incubation

Nest Locations

Data concerning nest locations are summarized in Table 24. Seventeen of the 22 nests (77.3%) were in mixed hardwood and oak habitats. These two habitats comprised only 33.34% of the study area, suggesting that they were selected in a non-random manner. The forest floors of both are quite open during the time of nest initiation. Shrubs are sparse and almost no new herbaceous cover is present. The frequent placement of grouse nests in habitats without dense ground cover has been noted by other workers (Bump et al., 1947; Edminster, 1947; Kupa 1966; Clarke, 1936; Moulton, 1968). The openness apparently enables the hen to observe potential predators and also gives her an avenue of escape. Most nests were at the base of a tree. The species and size of tree selected

Table 24. Nest location data.

Bird No.	Habitat Located in	Relationship to Solid Object		Direction Nest Faces	Habitat Edge Near Nest	Distance from Nest to Edge (ft)	% Standing Water Within 33x33ft Quadrat
		Species	DBH (in)				
1657	tamarack	Am. elm	3.2	NW	none	-	20
1684	oak	oak deadfall	-	-	oak:open meadow	18	0
1690	mixed hdwds	alder	2.5	NE	none	-	85
1691	oak	none	-	S	oak:open field	18	10
1695	mixed hdwds	aspen	5.1	SW	mixed hdwd: cnty road	21	0
1697	oak	red oak	10.5	E	oak:open meadow	21	0
1698	oak	red oak	7.3	N	none	-	0
1699	mixed hdwds	red maple	7.6	SW	none	-	60
2200	mixed hdwds	white birch	4.5	S	none	-	0
2201	oak	red oak	11.5	N	oak:dirt road	12	0
2202	oak	red oak	8.3	SE	oak:open field	6	0

Table 24. Nest location data. (continued)

Bird No.	Habitat Located in	Relationship to Solid Object		Direction Nest Faces	Habitat Edge Near Nest	Distance from Nest to Edge (ft)	% Standing Water Within 33x33ft Quadrat
		Species	DBH (in)				
2210	mixed hdwds	white birch	5.4	E	none	-	5
2219	white birch	white birch	5.7	SW	none	-	0
2235	oak	red oak	9.3	S	oak:county road	3	0
2238	mixed hdwds	white birch	5.1	S	none	-	35
2239	mixed hdwds	none	-	W	none	-	0
2241	oak	red oak	7.3	NW	none	-	0
2245	mixed shrubs	none	-	W	none	-	50
2246	mixed hdwds	alder	2.2	N	mixed hdwds: open field	30	0
2248	mixed hdwds	white birch	5.1	SE	none	-	35
"A"	aspen	aspen	-	SW	aspen:open field	15	0
"B"	aspen	aspen	-	E	none	-	0

varied, depending largely on what was available in the nesting area. One nest was placed under the brushy end of an oak deadfall. Three were not placed near trees or other solid objects. In relation to the tree or to slope when the nest was not at the base of a tree, nests faced all directions. However, the hens appeared to favor the south and southwest, suggesting a slight preference for sunny places.

Bump et al. (1947) and Edminster (1947) reported that many of their nests were within 100 feet of an opening in the woods. In the present study 9 nests (40.9%) were within 30 feet of openings.

Kupa (1966) reported that most grouse nests found at Cloquet were in upland habitats. At Cedar Creek 7 nests were in habitats containing considerable amounts of standing water within a 33 foot by 33 foot quadrant around the nest. Whether the high grouse populations during the present study affected the location of nests is not known. However, nests in wet areas are easily overlooked and may be more common than is generally believed, since lowlands usually are more difficult for humans to traverse. Probably most nest searching or other activities which lead to the chance finding of a grouse nest are conducted in upland areas. In the present study, 6 of 8 nests of previously unmarked hens were found in upland types (4-oak, 2-aspen). Only 6 of 14 nests of previously radio-marked hens were in upland habitats.

Habitat Usage

Since the areas utilized by hens during the incubation period were quite small (Table 8), the grid-square method of vegetation analysis, as used during other time periods, tended to reflect the habitat type within which the nest was located. However, field observations of hens while off the nest feeding revealed a different situation. For example, on 18 May, 1972 Hen 2239 was observed to leave its nest and fly directly to a white cedar swamp, a habitat normally avoided by the birds (Fig. 10). When this bird was relocated with a portable receiver, it was feeding in a lone trembling aspen surrounded by scattered white birch and cedars. No other aspens were visible from that point.

A marked preference for trembling aspen as a food source is readily apparent from Table 25 which summarizes the field locations of hens while feeding away from the nest. This is in agreement with the findings of Schladweiler (1968), except that he found that only male aspens were utilized. No preference for male aspens was noted at Cedar Creek. Most birds fed in female trees at a time when new leaves were emerging. Most male catkins had fallen by then while female catkins were attaining full size. The hens apparently ate mostly leaves, but female catkins were also eaten.

Table 25 shows that grouse hens seldom fed in aspens closest to the nest. Hens flew as far as 185 yards to a feeding site, and according to the film record and TV monitor observations, they left the nest only to feed. Selected feeding sites were utilized

Table 25. Field locations of feeding grouse hens during the incubation period.

Bird No.	Date	Time	Species Feeding Upon	D.B.H. (Inches)	Distance From Nest (Yards)	Distance From Nest To Nearest Aspen (Yards)
1691	3 Jun 71	12:45-12:50	T. Aspen (male)	-	28	28
2241	12 May 72	18:43-18:51	T. Aspen (female)	-	185	35
2241	15 May 72	04:15-04:35	T. Aspen (male)	6.4	185	35
2235	15 May 72	19:27-19:57	T. Aspen (female)	-	75	25
2219	16 May 72	19:10-19:15	T. Aspen (female)	-	57	10
2246	17 May 72	04:00-04:45	T. Aspen (male)	7.5	70	70
2239	18 May 72	04:05-04:21	T. Aspen (?)	5.0	110	80
2210	18 May 72	19:15-19:40	T. Aspen (male)	8.6	110	45
2238	19 May 72	04:10-04:23	T. Aspen (male)	5.4	48	5
2245	19 May 72	18:45-18:50	T. Aspen (female)	1.9	55	30
2241	22 May 72	04:10-04:26	Am. Elm	6.4	150	35
2235	22 May 72	19:15-19:25	T. Aspen (?)	2.9	75	25
2219	23 May 72	19:40-20:00	T. Aspen (female)	-	57	10
2248	26 May 72	04:45-04:53	T. Aspen (female)	5.1	93	14

repeatedly, although all hens monitored typically used several different feeding sites during the incubation period.

TV Observations of an Incubating Hen

Over a 16 day period, Hen 2219 was observed by a TV monitor leaving its nest to feed and returning after feeding periods a total of 12 and 17 times respectively. Departures from the nest were markedly uniform. In all observed instances the hen stood up, walked a short distance in the same direction each time, and flew to a feeding site, usually a clone of female aspens 55 yards from the nest. These flights began 1.5 feet (8 times), 2.5 feet (3 times) and 4 feet (once) from the nest. No attempt was made by the hen to cover the eggs. This was also the case at all other nests observed while the hen was absent.

Return trips to the nest were much less uniform. Thirteen times the hen walked into the TV field of view (an area of about 5 feet on either side and in front of the nest), likely after having landed near the nest outside the picture area. Twice the bird landed within 2 feet of the nest and 3 times within 4-5 feet. During these returns the hen approached the nest from various directions. Typically, the hen walked directly to the nest and settled on the eggs within a period of 30 seconds. The incubating hen usually remained completely motionless. Occasionally it shuffled around on the eggs for a few seconds, and at times was observed to turn an egg or two. In general these observations agree with those of Bump et al. (1947), who observed 2 nests over

a three-day period.

Captive Chicks

Growth rates of the 9 grouse chicks raised in captivity (Table 26) were well ahead of those reported by Bump et al. (1947), but were roughly comparable to those reported by Fay (1963). Males remained heavier than females throughout the growing period.

Newly hatched chicks were somewhat wobbly on their legs for the first few hours following hatching. Little food was actually consumed the first day, although the chicks pecked at small insects that moved about. They also pecked at conspicuous inanimate objects such as spots on their cardboard box cage. In the beginning, these pecking movements were poorly coordinated, and a chick frequently made several attempts before hitting the object. By the end of the first day most chicks walked strongly and ate small insects. By the second day the chicks actively fed on insects. They jumped 6 1/2 inches in attempting to catch insects on the screen cover of their box. By the morning of the third day the chicks were capable of jumping out of the box.

Although the chicks developed seemingly insatiable appetites and consumed large quantities of insects daily, they were somewhat selective in the insects they would eat. Flies (Diptera), grasshoppers (Orthoptera), dragonflies, damselflies (Odonata), caterpillars, butterflies, small moths (Lepidoptera) and leaf bugs (Miridae) were readily consumed. However, stink bugs (Pentatomidae), small ground beetles (Carabidae), small scarab

Table 26. Growth rates of captive Ruffed Grouse juveniles.

Date	Age (Weeks)	Individual Weights (Grams)								Average		
		Females					Males				Weights (Grams)	
		YL	YR	GR	BL	PR	AL	RL	BR	GL	Females	Males
14 Jun	2	53	47	50	44	44	55	53	53	47	48	52
22 Jun	3	97	91	91	80	87	108	103	116	94	89	105
30 Jun	4	153	142	141	132	145	174	164	167	150	143	164
6 Jul	5	201	194	187	178	195	232	221	233	204	191	222
13 Jul	6	260	244	246	223	247	298	279	303	265	244	286
20 Jul	7	325	290	315	283	315	373	337	377	330	306	354
28 Jul	8	352	330	350	315	342	422	382	424	380	338	402
3 Aug	9	413	383	420	357	403	488	433	495	443	395	465
10 Aug	10	440	405	457	400	430	517	474	527	484	426	500
17 Aug	11	472	432	474	420	462	564	507	560	522	452	538
24 Aug	12	482	455	485	435	497	585	527	585	522	471	562
31 Aug	13	519	482	509	456	522	619	557	622	575	497	593
7 Sep	14	522	492	514	480	504	637	557	624	604	502	605
14 Sep	15	515	470	500	465	500	610	532	547*	572	490	571**
21 Sep	16	530	497	508	485	502	630	563	557*	590	504	594**

* Leg injured.

** Weight of BR not used in calculation of average.

beetles (Scarabaeidae), and ants (Formicidae) were eaten only when the chicks were very hungry. On numerous occasions insects in the latter group were observed crawling unmolested inside the chick's cardboard box cage. When the chicks were moved to an outdoor enclosure, ants were frequently observed crawling about inside, but were usually ignored by the ever-hungry chicks.

The chick's primaries, already visible at hatching, grew rapidly. At the age of one week they were 2.3 in long and capable of supporting the chicks in flight for short distances. Development of their body plumage was similar to that described by Bump et al. (1947).

Brood Flushes

Brood flushes are summarized in Table 27. The number of chicks seen when a brood flushed depended on several variables. Small, flightless chicks scattered and hid making accurate counts difficult. Flying chicks were easier to count, although the amount of concealing vegetation was an important factor. Despite the fact that it was not possible to count all the chicks for each brood flush, it was obvious that the number of chicks declined gradually as the season progressed. There were two exceptions. Hen 2235 appeared to have only 4 of 10 chicks remaining when flushed from relatively open cover on 5 July, 1972. On 4 occasions during 1-14 August, it flushed with 10-15 young of similar size. Likewise Hen 2239, which hatched 9 eggs, flushed from an open field with at least 13 young of similar size on

Table 27. Brood flushed.

Bird No.	Date Flushed	Age of Chicks (Days)	No. of Chicks Seen	Remarks
1657	3 Jun 71	1	2	Hen flew 3 yds., mewed.
	9 Jun 71	7	3	Hen flew 3-6 yds., mewed.
	15 Jun 71	13	0	Hen flew 10 yds., mewed several times.
	21 Jun 71	19	2	Hen flew 10 yds., mewed several times.
	28 Jun 71	26	3	Hen flew 10 yds., mewed several times, began peeping a few minutes later.
	30 Jun 71	28	6	Hen flew off.
1690	9 Jun 71	5	3	Hen flew about 17 yds., no display.
1691	9 Jun 71	5	0	Hen flew 10 yds., mewed, walked back peeping.
	10 Jun 71	6	1	Hen ran off, mewed.
	14 Jun 71	10	2	
	21 Jun 71	17	0	Hen flew off.
	23 Jun 71	19	1	Hen flew 10 yds., mewed several times.
	30 Jun 71	26	1	
	2 Sep 71	90	1	Hen flew off.
1695	13 Jun 71	1	0	Hen flew off, no display.
	22 Jun 71	4	2	Hen not flushed.
1699	31 May 71	2	10	Hen rushed observer, hissed and displayed.
	2 Jun 71	4	1	Hen rushed observer, hissed and displayed.
2200	2 Jun 71	2	2	Hen flew several yards, rushed observer hissing and displaying, flew off.

Table 27. Brood flushes. (continued)

Bird No.	Date Flushed	Age of Chicks (Days)	No. of Chicks Seen	Remarks
2200	6 Jun 71	6	0	Hen flew off, returned and rushed observer hissing and displaying, flew off.
	9 Jun 71	9	8	Hen flew off, mewed several times, began peeping.
	17 Jun 71	17	6	Hen flew off, no display.
	18 Jun 71	18	1	Hen flew off, no display.
	29 Jun 71	29	2	
	30 Jun 71	30	6	
	26 Jun 71	56	4	
2235	7 Jun 72	2	0	Hen flew weakly 10 yds., mewed.
	20 Jun 72	15	5	Hen flew weakly 10 yds., mewed.
	27 Jun 72	22	5	Hen flew 10 yds., low to ground, mewed several times.
	5 Jul 72	30	4	Hen flew 7 yds. low fluttering flight, mewed.
	1 Aug 72	57	12	Hen flew several yards, low fluttering flight.
	7 Aug 72	63	15	Hen flew off, no display.
	8 Aug 72	64	15	Hen flew off, no display.
	14 Aug 72	70	10	Hen flew off, no display.
2238	14 Jun 72	5	0	Hen flew several yards, mewed.
2239	16 Jun 72	10	8	Hen not flushed.
	26 Jun 72	20	9	Hen flew off, no display.
	3 Jul 72	27	13	Hen flew off, no display.

Table 27. Brood flushes. (continued)

Bird No.	Date Flushed	Age of Chicks (Days)	No. of Chicks Seen	Remarks
2246	16 Jun 72	9	0	Hen rushed observer hissing and displaying, flew off 7 yds., mewed, feigned injury, led observer away from brood, finally flew off.
	25 Jun 72	18	7	Hen flew off, no display.
Unmarked	11 Jun 71	-	0	Hen rushed observer hissing and displaying, feigned injury.
	12 Jun 71	-	0	Hen rushed observer hissing and displaying.
	12 Jun 71	-	1	Hen rushed observer hissing and displaying.
	17 Jun 71	14*	3	Hen flew several yards, mewed.
	20 Jun 71	7*	1	Hen rushed observer hissing and displaying, hopped upon low branch, peeped.
	21 Jun 72	10*	2	Hen rushed observer hissing and displaying, flew weakly 10 yds., mewed and peeped.
	21 Jun 72	14*	8	Hen not flushed, heard peeping.
	21 Jun 72	10*	2	Hen flew off weakly.
	4 Jul 72	-	7	Hen flew off, low fluttering flight.
	27 May 73	1	11	Hen ran off, no display. Chicks still in nest.
	4 Jun 73	1	14	Hen ran off, feigned injury, mewed, rushed observer several times hissing and displaying, attempted to lead observer away. Chicks still in nest

* approximate age.

3 July, 1972. On none of these occasions was a second adult seen with the brood. There can be no doubt that these hens acquired extra chicks.

Bump et al. (1947) reported that they had encountered double broods on a number of occasions, usually when both hens were present. They also believed that broods merge permanently at times, particularly if one of the hens is killed. Hungerford (1953) reported a communal brood of two hens accompanied by about 15 young. Chambers and Sharp (1958) captured a group consisting of 2 hens and 5 chicks of 2 age classes. They also observed other groups containing young of different ages, and further reported that mixing of broods occurred more frequently as the summer progressed.

At Cedar Creek the reactions of individual brood hens when flushed was similar to that described by Bump et al. (1947) and Johnsgard (1973). Hens attending small chicks often rushed the observer, hissing loudly, with tails elevated and spread, ruff erected, and wings dropped -- a display very similar to the strutting display of male grouse described by Allen (1934) and Hjorth (1970). On other occasions hens flew off short distances and gave a series of mewing squeals. Sometimes they attempted to lead an observer away by feigning injury. As the chicks grew older and able to fly, the reaction of the hens gradually changed. Hens no longer rushed the observer. Occasionally hens flew off a short distance in a low, fluttering flight, and began mewing. More often the hen and brood simply flew off.

DISCUSSION

Effects of the Transmitter on Behavior

One of the major concerns of a telemetry study is that the transmitter may cause behavioral changes in the study animals. Since many telemetry studies are conducted on animals difficult to observe in the wild, the effects of the transmitter on behavior are difficult to determine. Boag (1972) stated that activity levels as well as food intake by captive female red grouse (Lagopus l. scoticus) were lower among radio-marked birds than controls, especially during the first week after transmitter attachment. At Cedar Creek all properly fitted transmitter harnesses had no noticeable effects on behavior of Ruffed Grouse. The harnesses fitted so well that within a short time after release only the whip antenna on the bird's back was visible. All of these grouse excluding those injured in traps apparently walked and flew normally. Observations of radio-marked captive grouse by Huempfer (unpublished data), confirmed this belief. Other researchers, e.g., Archibald (1973), Barrett (1970), Schladweiler (1965) and Godfrey (1967) stated that the behavior of radio-marked grouse was not noticeably different from that of unmarked birds.

In the present study, however, problems occurred with three brood hens (Nos. 1657, 1690, 1695) during the 1971 season. The transmitter harnesses had been fitted loosely to allow for weight gain following incubation. These hens apparently were not able

to free one of their legs that became entangled under the harness loop passing across the bare brood patch. Data taken from these hens after the mishap were not used in the analysis. The problem was corrected in 1972 by fastening the transmitters more snugly. The importance of recapturing marked animals periodically to assess possible adverse effects of the transmitter cannot be overstated.

Activity

Little detailed information is available in the literature on activity periods of Tetraonids in the wild. Huempfer (unpublished data) found that mid-day activity of Ruffed Grouse during the winter months was substantially lower than mid-day activity levels recorded during the present study. Brander (1965) reported that radio-marked Ruffed Grouse roosted at sunset and left the roost about 30 minutes before sunrise during March and April. His birds were inactive from mid-morning until mid-afternoon particularly through the end of March. The inactive periods probably reflect the need of the birds to conserve energy during the winter months. Schladweiler (1965) stated that Ruffed Grouse generally began activity 1/2 to 1 hour before sunrise and ceased activity 1/2 to 1 hour after sunset during the breeding season. Once activity began, the birds tended to remain active most of the day without any prolonged inactive periods. Weather disturbed them little except during those times when chicks were small. Probably a transition from prolonged mid-day inactive

periods (Huempfer, unpublished data; Brander, 1965) to few inactive periods during daylight hours (Schladweiler, 1965; the present study) occurs during spring as temperatures increase and snow cover disappears.

The relationship between dawn and dusk activity peaks found at Cedar Creek in the present study, as well as those of Archibald (1973) and Pierson and Tester (unpublished data) in which the dawn peak is usually smaller than the dusk peak may prove to be the normal pattern throughout the year. These morning and evening activity peaks are probably associated with feeding periods. Archibald (1973) observed male grouse feeding in trembling aspen clones during these times. In the present study, female grouse were observed feeding in aspen clones during the morning and evening activity peaks on several occasions.

Incubation

Skutch (1962) stated that in most cases where only one parent incubates, the eggs are covered 60 to 80% of the daytime. Tetraonids of several species exhibit a higher percentage of nest attentiveness than reported by Skutch (1962). In the present study grouse hens averaged 95.7% of the incubation period on the eggs. Kupa (1966) stated that Ruffed Grouse hens spent an average of 23 hours and 12 minutes (96.7%) on the nests each day. Lennestedt (1966) recorded the activity of a Capercaillie (Tetrao urogallus) hen during 12 days of its incubation period and reported that it was off the nest only 4.9% of the time.

McCourt et al. (1973) stated that 2 incubating Spruce Grouse consistently spent 93% of the daylight hours on the nest.

Lennekstedt (1966) reported that activity periods of an incubating Capercaillie were fairly evenly distributed throughout the day except from 1800-2300 hours when no absences occurred. Although his study was conducted under conditions of continuous daylight, the onset of activity periods between 0300-0600 hours gradually shifted from slightly after 0300 to about 0520 over the period of study. This shift is similar to the shift in morning activity onset observed during incubation in the present study (Figure 4a, b, c). McCourt et al. (1973) recorded activity periods of a female Spruce Grouse during the last 7 days of its incubation period. Although nearly complete data were obtained only during one of the 7 days, they concluded that the hen fed 6 times daily on a relatively rigid schedule. If female Spruce Grouse undergo any change in activity periods during incubation, as do the Ruffed Grouse at Cedar Creek, their overall pattern of activity during incubation probably is substantially different from that reported by McCourt et al. (1973).

Home Range

Many studies of the Ruffed Grouse have reported movement or home range data during various times of the year. Most estimates of range size, except for recent telemetry studies, have been based on little data. Males are more sedentary than females (Archibald, 1973; Chambers and Sharp, 1958; Gullion, 1970; Hale

and Dorney, 1963; Rusch and Keith, 1971b), probably because of the close attachment to drumming sites. Broods typically remain together until late summer or early fall at which time the juveniles disperse. Dispersals of a mile or more are common. Individuals occasionally travel 7-8 miles from their brood range (Godfrey and Marshall, 1969; Hale and Dorney, 1963; Chambers and Sharp, 1958). After dispersing, the birds become relatively sedentary.

Data from the present study (Table 8) indicate that female grouse tend to use relatively large home ranges for several weeks prior to the onset of egg-laying. Archibald (1973) reported a marked increase in home range size of three hens for several weeks before incubation onset. During the pre-egg-laying period, according to Brander (1967), home range size tends to reflect movements of hens to the activity centers of one or more drumming males.

During the egg-laying period Schladweiler (1965) recorded home ranges of 3 hens ranging from 10-35 acres -- a figure almost identical to the range of 10.07 - 34.56 acres for 9 hens in the present study (Table 9). Schladweiler (1965) recorded a 3 1/2 - 4 acre home range for a hen during incubation. This figure is slightly larger than that obtained for most hens at Cedar Creek where movements during the incubation period were confined to flights to and from feeding locations. In reality, the home range during incubation consists only of the nesting site and one or more feeding sites.

Many estimates on the movements of hens with broods are present in the literature. In past years most observers felt that young grouse do not move far from the nest. Forbush (1927) reported that broods never go far from the nest. Eng (1959) stated that the nest location determines the area where broods reside. Sharp (1963) stated that chicks under 10 days of age are relatively immobile. Fisher (1939), Polderboer (1942), Hungerford (1957), Chambers and Sharp (1958), and Rusch and Keith (1971b) all stated that young grouse utilize a relatively small range. According to Bump et al. (1947) most brood ranges are less than 100 acres and average about 40 acres. Edminster (1947) reported that the average brood range is about 1/4-mile in diameter, whereas Chambers and Sharp (1958) stated that broods utilize areas not exceeding a 1/4-mile radius. Schladweiler (1965) reported home ranges of 35-40 acres for one hen and approximately 400 acres for another during the first two weeks after hatching. The present study shows that grouse chicks become very mobile by the second day and that during the first 4 to 5 weeks following hatching hens with chicks are relatively more mobile than hens without broods (see Figures 8 and 9). These observations agree with Barrett (1970) who stated that chicks are capable of moving long distances by the second day. Bump et al. (1947) banded a brood at the nest and located it 1/2-mile from there 24 hours later. Young chicks obviously are capable of moving long distances.

Sanderson (1966) pointed out that the size and shape of an animal's home range are of limited significance. Of greater importance are the ecological factors which determine the home range of an animal. The differences in range size during the post-incubation periods recorded in the present study (Figures 8 and 9) probably reflect biological factors. In spite of the chicks' rapid growth and development, broods are relatively less mobile during the first week than other periods. The increase in range size through the third week probably reflects the increasing mobility of the brood members as well as their increasing food requirements. Several authors, (e.g. Bump et al., 1947, Edminster, 1947; Stewart, 1956) have noted that young Ruffed Grouse feed largely on insects for the first few weeks of life and then gradually shift to a diet primarily composed of plant materials.

As the broods grow older they may need to cover larger areas in order to obtain sufficient quantities of insects. The decrease in range size after the third week probably reflects the gradual changeover from insect to plant foods. Phenological records indicate that proper plant food is abundant by the time changeover takes place.

Hen 1691 consistently used smaller areas than the other brood hens, possibly because only 2 of her chicks remained by the end of the second week, and only one survived by the end of the third week. A small area likely contains sufficient food for only one or 2 chicks whereas the same area might not support a

more typical brood of 4 to 8 young.

Little has been written about hens without broods. Their movements during the first week after nest destruction probably reflect a difficult period of physiological adjustment from a reproductive to a non-reproductive status. Conceivably these hens respond to the drumming of males but few apparently attempt renesting. With few exceptions (Hen 2241) hens without broods used small areas after the first week. Numerous potential plant foods were available by that time enabling a broodless hen to obtain sufficient food within the small area.

Haas (1974) found that female Spruce Grouse without broods tended to move over smaller areas than hens with broods. In contrast, Braun and Rogers (1971) found that female White-tailed Ptarmigan (Lagopus leucurus) without broods wandered widely while those with broods, once in brooding areas, tended to be sedentary.

Vegetation Usage

Utilization of Aspen

The low usage of aspen (Figure 10) except during incubation may seem surprising, since many studies have shown this tree species to be an important food source of the Ruffed Grouse throughout the year, e.g., Svoboda and Gullion (1972), Vanderschaegen (1970), Huff (1970), Brown (1946), Korshgen (1966), and Schladweiler (1968). However, the low utilization of aspens recorded during the present study does not necessarily indicate that grouse hens were not feeding on them. Grouse feeding periods

in aspen are normally brief, only 15-20 minutes, according to Gullion and Svoboda (1972). Aspen clones tend to be rather scattered over the Cedar Creek area. If a grouse moved from a non-aspen type to an aspen clone to feed for 15-20 minutes, and then returned to a non-aspen habitat to roost, etc., only one or 2 radio fixes would have been recorded in the aspen habitat. Since scattered aspens are found in several of the habitat types, a feeding period in one of these trees would not be recorded as usage of aspen.

Field observations of both marked and unmarked grouse at Cedar Creek indicated that aspen was a preferred food source at least during the pre-incubation and incubation periods. The dense foliage present in most habitats by the time of hatching made visual observations of feeding grouse virtually impossible. The importance of aspen to female grouse in this study was probably greater than indicated by the grid-square method of habitat analysis.

Habitat Usage by Broods

Many observers have studied habitat usage of Ruffed Grouse broods. Bump et al. (1947), Edminster (1947), Polderboer (1942), Hungerford (1951, 1953), Sharp (1963), Porath and Vohs (1972), King (1937) and Stewart (1956) reported rather extensive use by young broods of openings or edges adjacent to openings in the forest. A similar usage of openings or forest edges was found in the present study. The white birch habitat, usually consisting

of a narrow strip of birches between open field and mixed hardwood habitats, received its greatest usage by broods (Figure 10). Although the open field habitat tended to be avoided throughout the study period, it nevertheless received its greatest usage by broods. On a number of occasions both marked and unmarked broods were flushed in an open field or along a white birch habitat edge adjacent to an open field. Schladweiler (1965) reported that at Cloquet young broods used upland types and avoided lowland habitats. Barrett (1970) also found at Cloquet that young broods preferred hardwood and hardwood-conifer types, but avoided jack pine and lowland habitats. Many authors, including King (1937), Eng (1959), Kupa (1966), Barrett (1970), Bump *et al.* (1947), Dorney (1959) and Hungerford (1951, 1953) reported a general shift from upland to the typically more dense lowland habitats by broods approximately 2-5 weeks of age. In contrast, Stewart (1956) reported a shift of broods from moist forests to drier forest types in Virginia. Rusch and Keith (1971a) found most of their broods in aspen habitats but none in alder or lowland thickets in Alberta. Aspen types in Alberta were found to have higher densities of shrubs than any other type present.

At Cedar Creek there was a strong preference by young broods for the mixed hardwood type (Figure 10). When its use decreased, the preferential use of lowland tamarack rapidly increased. Only one brood hen (No. 2235) made extensive use of the oak uplands. Use of alder lowlands by young broods did not appear to be preferential in relation to its availability.

Moulton (1968), in reference to Ruffed Grouse, states that "habitat that birds less than 4 weeks old pass through to reach brood habitats should not be confused with the more important habitat that holds juveniles over summer". On the contrary, the first few weeks are the most critical period in the life of a grouse. Habitats used during this period are very important to the survival of the chicks. The shift in habitat usage by broods reflect changing mobility and food habits of the brood members rather than simply a passage through various habitats in search of "brood habitats" as Moulton (1968) implies.

Habitat Usage by Broodless Hens

The literature contains little data concerning habitat usage by hens without broods. Schladweiler (1965) reported the use of alder habitats. Berner and Gysel (1969) stated that in summer adult males and broodless hens used cover types similar to those used by drumming males in spring, i.e. lowland hardwoods, aspen, and aspen-hardwood mixtures. The present study indicates that hens without broods used alder habitats extensively. Dense alder vegetation at Cedar Creek is similar to the molting cover described by Kind (1937) and Grange (1948).

Ecological Comparison of Hens With and Without Broods

The present study indicates that during the post-incubation period Ruffed Grouse hens with broods are less active, use larger home ranges, occupy different habitats, and suffer higher

mortality than hens without broods. Lower activity levels of brood hens (Table 5) reflect the necessity of attending chicks during the early stages of the brood period. The larger home ranges utilized by brood hens (Figures 8 and 9) probably indicates that their broods must cover a large area to find sufficient insect food. A broodless hen, primarily a vegetarian, can satisfy all its food requirements within a small area. Differences in habitat utilization (Figure 10) reflect ecological requirements of the two groups. Clarke (1936), Schladweiler (1965) and Porath and Vohs (1972) stated that young broods avoid dense brush or habitats with extremely dense ground cover. Observations at Cedar Creed are in agreement. The mixed hardwood and white birch habitats preferred by young broods usually contain dense ferns. In many places the ferns form a nearly continuous canopy a foot or more above the ground. Under this canopy the vegetation is relatively open, allowing grouse chicks to move about freely at ground level. On the other hand, the alder habitat preferred by broodless hens usually contains a wet, dense, herbaceous growth unsuitable to chicks at ground level.

The high mortality rate suffered by brood hens during the study period (e.g., 4 of 9 brood hens were killed by predators as opposed to no mortality suffered by 6 broodless hens) was probably due to a combination of factors. A hen accompanied by a number of active, noisy chicks runs a greater risk of being discovered by a predator than a lone individual. Grouse chicks can be heard calling at a distance of at least 30 yards. The

less dense habitats used by hens with broods also increase the risk of predation. Brood hens also run a risk in giving distraction displays in the presence of predators. In addition, they are not in peak physical condition and seem more vulnerable to capture at this time.

The alder habitat used by broodless hens at Cedar Creek consists of a dense canopy formed by the alders in addition to a dense understory of herbaceous vegetation, providing a ready source of food and cover. Nicholls and Warner (1972) found that radio-marked Barred Owls avoided the alder swamp habitats at Cedar Creek, presumably because of the difficulty they had in finding and pursuing prey in the dense vegetation. It may be that most avian and mammalian predators avoid this habitat. The oft-noted shift of grouse broods from upland to lowland habitats as the chicks become increasingly vegetarian may in fact be a movement to more secure habitats.

Although the activity patterns, movements, and habitat usage of a brood hen apparently increase its likelihood of being preyed upon in comparison to a broodless hen, these behaviors must be beneficial to the chicks or they would not be selected for. Also, the high fall and winter mortality of 55% normally suffered by this species (Gullion, 1970) indicates a strong selection pressure for a hen to rear a brood during its first breeding season as relatively few will receive a second chance.

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