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Breeding Season Movements and
Habitat Use of Female Sharp-tailed Grouse

by

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BREEDING SEASON MOVEMENTS AND
HABITAT USE OF FEMALE SHARP-TAILED GROUSE

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A dissertation submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of

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ABSTRACT

Movements, home ranges and habitats used by 24 female Sharp-tailed Grouse (Pedioecetes phasianellus (Linnaeus)) were determined using radio telemetry during the breeding seasons of 1976 and 1977, near Chatfield, Manitoba.

During the pre-incubation period some females moved long distances ($\bar{x} = 1.51$ km) from capture arenas and visited other arenas. These females had significantly larger home ranges than presumed non-dispersing birds. Habitats were not used at this time relative to their availability. Forest and shrub habitats were used most often. Nest sites had taller, denser shrub cover than randomly sampled sites in the same habitat type. Incubating females moved short distances (<150 m) from nests to feed and used the same feeding sites repeatedly. Home ranges of brood-rearing females were significantly larger than broodless females. Females with broods used mainly grasslands or grass-shrub areas. Broodless females used shrub and forest areas most often. Habitats were not used in proportion to their availability by either group. There was a significant difference in the density of cover used during the day by brood-rearing females. Open areas were used in mornings and evenings,

dense cover at mid-day and moderately dense cover at night roosts. Brood sites seemed to be selected in relation to cover and site temperature.

Dispersal, home range overlap and the effects of weather on home range, movements, and cover and habitat selection are also discussed.

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INTRODUCTION

Animals seek optimal environmental conditions. This behaviour has been equated to shelter seeking and is associated with selection of particular cover or habitat types for different activities (see Leopold 1933). Studies of habitat use in birds indicate selection is based on the structure or physiognomy of the habitat (MacArthur and MacArthur 1961, Hilden 1965). Therefore, knowledge of the height, form and spatial distribution of the vegetation is essential in understanding the ecological requirements of a species.

Plasticity in habitat requirements has been illustrated in several species of birds (Lack 1972). The Sharp-tailed Grouse (Pedioecetes phasianellus) is considered an inhabitant of the grasslands, forest-prairie ecotone, and deciduous forests (Aldrich 1963, Johnsgard and Wood 1968). Work over the last 30 years has provided general information on the habitat requirements of this species in various parts of its range (Aldous 1943, Grange 1948, Hart et al. 1953, Amman 1957 and others). Evans (1968), in reviewing Sharp-tailed Grouse habitat requirements, noted that habitats selected vary with season, age, and sex of the individuals examined.

In the Canadian Prairie Provinces Sharp-tailed Grouse are abundant, permanent residents (Aldrich and Duvall 1955, Aldrich 1963). Most studies of this species in Canada have been of the behaviour of males (Lumsden 1965, Evans 1969, Rippin and Boag 1974 a, b). Little information is available on spring and summer habitat requirements (Pepper 1972). Pepper (op. cit.) provided data on habitat requirements of Sharp-tailed Grouse in a grazed and farmed area of Saskatchewan which he considered lacked sufficient optimal habitat.

Information on pre-nesting habitat requirements of females is virtually non-existent (but see Marshall and Jensen 1937). Further, no published information relates habitat use to availability in an area. Post-nesting habitat used by broods has been described (Amman 1957, Peterle 1954, Hamerstrom 1963) although the data may be somewhat biased due to searching techniques and behaviour of broods (see Baumgartner 1939).

The early studies of Sharp-tailed Grouse movements relied on banding, colour-marking and recapture, or re-sightings (Hamerstrom and Hamerstrom 1951, Jackson and Henderson 1965, Schwilling 1961, Robel et al. 1972). These studies provided limited data and were most useful in determining dispersal patterns of particular individuals. Hamerstrom and Hamerstrom (1951) noted that summer movements of Sharp-tailed Grouse are essentially unknown.

Nesting studies indicated that females moved only short distances from arenas to nest (Hamerstrom 1939, Symington and Harper 1957). This prompted Blus and Walker (1965) to suggest that females must use available habitat close to arenas for nesting even if it was poor in quality. Robel et al. (1970) showed that female Greater Prairie Chicken (Tympanachus cupido) made inter-arena movements and are therefore not limited to nesting around a specific arena. Since Hamerstrom and Hamerstrom's (1951) important study on movements, Artmann (1970) and Christenson (1971) have provided limited data on home ranges and movements of female Sharp-tailed Grouse, but Johnsgard (1973) reported that information on these aspects is still inadequate.

Animals' home ranges and movement patterns depend on both behavioural responses to their own or other species and on characteristics of the available habitat (Moen 1973). In tetraonids, knowledge of habitat requirements, home range and movements is essential to understanding the ecology of the species and to permit their management (Archibald 1975).

Hamerstrom et al. (1952) have indicated that Sharp-tailed Grouse flourish in areas of bushy cover undisturbed by agriculture. With this in mind, it was determined that in an agriculturally undisturbed area of Manitoba studies using radio-telemetry could contribute information on many aspects of Sharp-tailed Grouse biology.

The objectives of this study were to determine for female Sharp-tailed Grouse: (1) dispersal patterns from arenas to nest sites, (2) habitat use prior to, during and after nesting, and (3) daily and seasonal home ranges and movements during the breeding season.

STUDY AREA

Location and Physiography

The study was conducted in a 27 km² portion of the Narcisse Wildlife Management Area near Chatfield, Manitoba (50°47' N, 97°34' W), in the Interlake Region, 90 km north of Winnipeg (Fig. 1). Agricultural history and development of the wildlife management area are described by Collins (1974).

The central Interlake is a relatively flat remnant basin of glacial Lake Agassiz (Weir 1960). The study area lies along the central ridge portion of the region (elevation 275 km) with the land sloping gently east and west towards Lakes Winnipeg and Manitoba, respectively. Lying across the general direction of the landfall is a ridge and swale topography oriented in a north-west and south-east direction resulting in poor drainage (Pratt et al. 1961).

Geology and Soils

The underlying bedrock of the region is Silurian dolomitic limestone of the Interlake Group (Baillie 1951). Near Chatfield exposed outcrops have been assigned to

Figure 1. Study area (outlined with broken line)
with insert showing location of
Chatfield in southern Manitoba.

the Inwood formation (Stearn 1956). A surface mantle of water-modified glacial till covers the bedrock. Soil coverage is variable; thin and stony on ridgetops and thicker in swales.

Near Chatfield soil types have been assigned to the Garson association and consist of gray wooded, dark gray, or peaty meadow soils (Pratt et al. 1961). Soils are generally thin (8-30 cm), stony, high in lime content and imperfectly drained.

Climate

The Interlake has a sub-humid continental climate with large seasonal temperature ranges (Weir 1960). Average summer temperatures are 15 C for June and 19 C for July. Mean annual precipitation is 50.8 cm, with half of this occurring as rain during spring and summer. The frost free period ranges from 90 to 100 days.

Vegetation

Chatfield is in the Manitoba Lowlands section of the Boreal Forest Region of Canada (Rowe 1973). Mixed forest predominates on undisturbed sites with adequate soil depth. The ridge and swale topography give rise to upland and lowland vegetation communities. The most frequently occurring plant species in the

Narcisse Wildlife Management Area are described by Collins (1974) and Rusch et al. (1976, 1978). Scientific names follow Scoggan (1957).

Trembling aspen (Populus tremuloides) is the dominant tree species. Bur oak (Quercus macrocarpa) and white spruce (Picea glauca) grow in scattered stands on well drained sites or ridgetops. Balsam poplar (Populus balsamifera) is present in low, moist locations. High lime content of soils and repeated fires have resulted in stands of stunted aspen over much of the area (Pratt et al. 1961). The patchy stands of scrubby aspen give the Chatfield area the appearance of aspen parkland (Bossenmaier and Vogel 1974).

Shrub species on upland sites include saskatoon serviceberry (Amelanchier alnifolia), chokecherry (Prunus virginiana), rose (Rosa spp.), shrubby cinquefoil (Potentilla fruticosa), Canada buffaloberry (Shepherdia canadensis), western snowberry (Symphoricarpos occidentalis), creeping juniper (Juniperus horizontalis), and bearberry (Arctostaphylos uva-ursi). In poorly drained areas or swales the common shrubs are willow (Salix spp.), high bush cranberry (Viburnum trilobum), dwarf birch (Betula glandulosa), and red-osier dogwood (Cornus stolonifera).

Upland grasses are predominantly needlegrass (Stipa spp.), wheat grass (Agropyron spp.), bluegrass (Poa spp.), and big bluestem (Andropogon gerardi). Reed grass (Calamagrostis spp.) and wild rye (Elymus canadensis) were

present in moist meadows and woodlands. Several cultivated hayfields and seeded trails also occur in the study area. They have been planted to sweet clover (Medicago sativa), alsike clover (Trilfolium hybridum) and intermediate wheat grass (Agropyron intermedium). The dominant emergents of marshes are cattails (Typha spp.), and sedges (Carex spp.).

Fauna

The avifauna of the area has been described by Taverner (1919), Norman (1920) and Cuthbert and Sexton (1976). Potential avian predators that occur as migrants or residents include Goshawk (Accipiter gentilis), Cooper's Hawk (A. cooperii), Sharp-shinned Hawk (A. straitus), Marsh Hawk (Circus hudsonius), Rough-legged Hawk (Buteo lagopus), Red-tailed Hawk (B. jamaicensis), Broad-winged Hawk (B. platypterus), Bald Eagle (Haliaeetus leucocephalus), Great Horned Owl (Bubo virginianus), and Snowy Owl (Nyctea scandiaca). Potential egg predators are Crow (Corvus brachyrhynchos) and Black-billed Magpie (Pica pica).

Rusch et al. (1976, 1978) report on some of the predatory mammals in the area. Personal observation and communication with local residents accounted for several others. They include coyote (Canis latrans), fox (Vulpes vulpes), short-tailed weasel (Mustela erminea), mink (Mustela vison), badger (Taxidea taxus), and striped

skunk (Mephitis mephitis). Thirteen-lined ground squirrels (Spermophilis tridecemlineatus) were also present and are known predators on grouse eggs (Patterson 1952).

METHODS

Seasonal Aspects

The study was conducted from early April through mid-August in 1976 and 1977. This period includes much of the breeding season of Sharp-tailed Grouse at this latitude (Artmann 1970). In this study I divided the breeding season into several periods. Pre-incubation is the period from when the females were released following capture at arenas until incubation started. It includes a pre-egg stage, the interval up to laying the first egg, and the egg stage, from laying the first egg to the onset of incubation. These periods were determined for each individual by backdating from the first day of incubation, knowing that eggs are laid approximately each day and allowing two days for days missed. (Artmann 1970, Johnsgard 1973, Maxson 1977). The incubation period extends from the onset of incubation until the last egg of a clutch hatches. Post-nesting is from hatching until late August when broods begin to disperse (Artmann 1970, Christenson 1971).

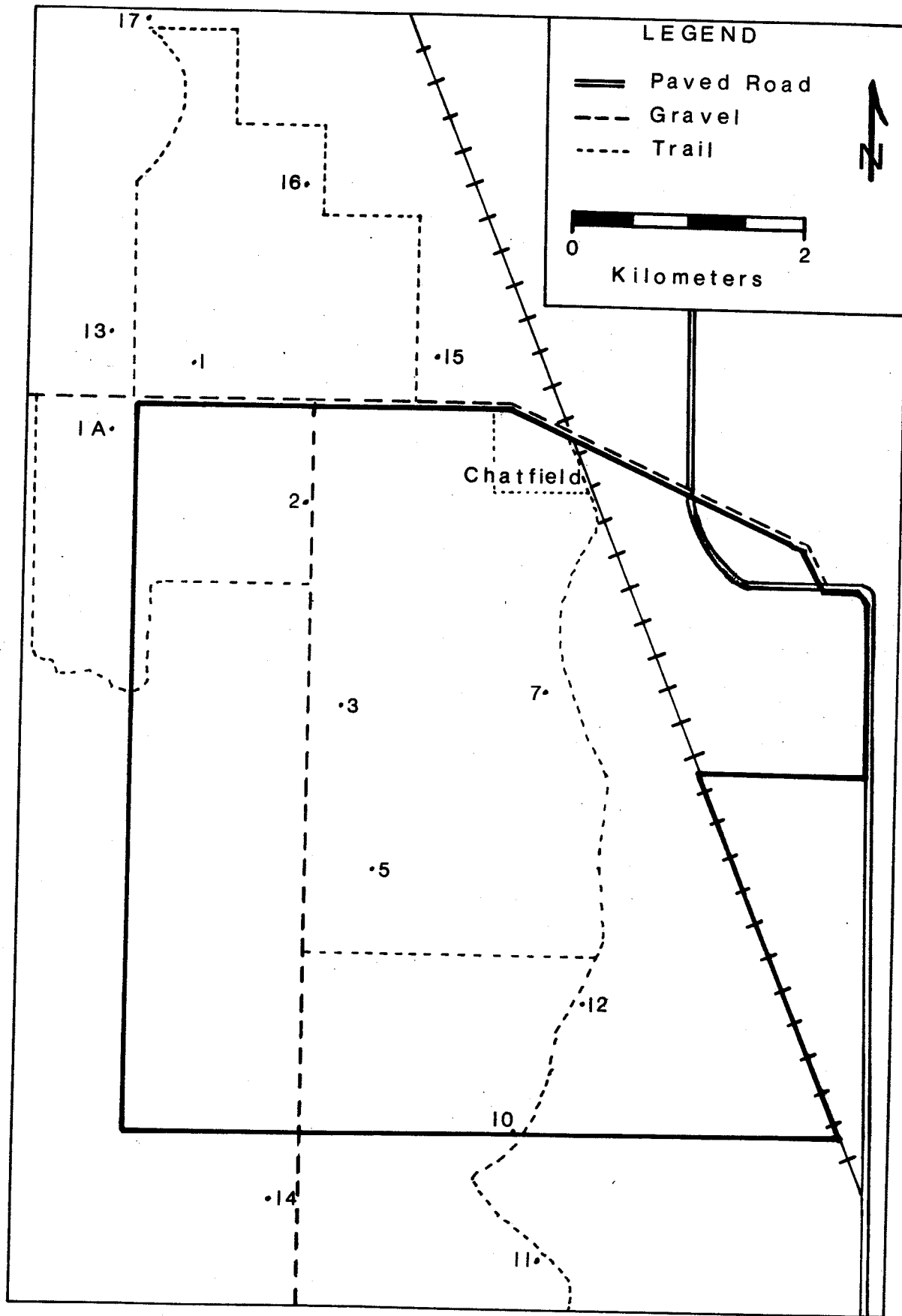
The post-nesting period was divided into two stages for comparative purposes. Young Sharp-tailed Grouse depend on the female for some time after hatching

(Caldwell 1976). Flight is not achieved until they are about 10 days old (Hart et al. 1953). Christenson (1971) suggests the first two weeks of life are critical for young Sharp-tailed Grouse, since most mortality occurs at this time. I examined movements and habitat use during the time when chicks were less than two weeks old to see if they differed from the remainder of the brood rearing period.

Trapping and Banding

Locations of arenas (sensu Hjorth 1970) were known from previous work in the area (Fig. 2) (M. Gillespie, pers. comm., McKay and Carmichael 1970). I observed arenas 2, 3 and 7 for several mornings beginning in early April. Areas where females concentrated, their approaches to arenas, and approximate locations of dominant males' territories on the arenas were recorded. Modified lily-pad or walk-in traps with short leads (<3 m) were placed across these approaches (Hamerstrom and Traux 1938, Liscinsky and Bailey 1955). Two opposed rocket nets were used on the two largest arenas in the study area. Each net was 18 m by 12 m, propelled by four rockets charged with solid fuel and activated by a 50 cap blasting machine situated in the blind. The nets were placed to cover areas where females concentrated, or the territories of dominant males.

Figure 2. Locations of arenas in the Narcisse Wildlife Management Area. Numbers correspond to those used in text.



Incubating females whose radios were to be changed were captured by flushing them into a mist net erected in a 'V' shape five to 10 m from the nest. Females with broods were caught in cloverleaf or lily-pad traps (Liscinsky and Bailey 1955, Gullion 1965).

Captured Sharp-tailed Grouse were sexed using crown and rectrix feather patterns (Amman 1944, Henderson et al. 1967). Attempts to age birds using Wright and Haitt's (1943) primary feather wear technique were abandoned early in the study. All birds captured showed worn outer primaries. Also, trapping methods, especially rocket netting, often damaged the tips of birds' primaries. Each grouse was banded with a numbered aluminum butt-end leg band (except for very small chicks) and released where captured.

Radio Telemetry

Radio telemetry has been used for various studies of galliforme birds, including Sharp-tailed Grouse (Artmann 1970, Bernhoft 1969, Brown 1966, Christenson 1971, McEwen and Brown 1966, Moyles 1977). McEwen and Brown (op. cit.) and Robel (1970 a) suggest that instrumented grouse are no more susceptible to predation than unmarked birds. Bowman and Robel (1977), Dumke and Pils (1973) and Mech (1967) have indicated its usefulness for studying predation and assumed their results are not

biased by the affects of the transmitter. Boag (1972) found that instrumented and non-instrumented Red Grouse (Lagopus lagopus scoticus) made similar use of different habitat types under captive conditions. He does indicate the birds took up to one week to become conditioned to the transmitter.

Twenty-four female Sharp-tailed Grouse were equipped with continuously emitting radio transmitters in the 150-151 MHz frequency range (Appendix 1). Transmitter components of the SM 1 type developed by AVM Instrument Company, Champaign, Illinois, were used. Mallory RM 640 mercury batteries provided the power source. Twist-flex stainless steel dental wire (various diameters) served as antennas. Components were assembled, coated in liquid latex and given two coats of 5-minute epoxy cement.

Harnessing techniques followed Brander (1968) with some modifications of Dumke and Pils (1973). Transmitters used in 1977 had the harness modified further by passing 22 gauge copper wire through poly vinyl chloride tubing and soldering one end to the positive battery tab. This facilitated better attachment to the grouse and improved the range of the transmitter (Herzog 1977). Transmitter weights ranged from 19.8 to 22.5 g and all were less than the recommended maximum 4% of the average female's body weight (Anon. 1975). Further, the heaviest transmitter weighed less than 4% of the lightest female weighed during the study.

To permit easier handling of grouse during instrumentation a dark hood made of porous cloth was placed over the bird's head. This reduced the bird's struggling and permitted both hands to be used to fit the transmitter to the grouse.

The locations of grouse were monitored using an LA 12 portable receiver (AVM Co.). This unit had 12 channels and three bands permitting up to 36 transmitters to be used per given area. Three types of antenna systems were employed to track birds. A hand-held three element antenna was used most often. The investigator walks in the direction of increasing signal strength and pinpoints the bird's location without disturbing it. By approaching the site from two directions, approximately 90° apart, the location can be determined to within one or two meters. The hand-held antenna method provided over 90% of locations of grouse in this study. Its range was about one km for birds on the ground.

A triangulation method was also employed (Marshall and Kupa 1963). A twin four-element directional yagi antenna on a vehicle-mounted, six meter telescoping mast was used. The intersection of two compass bearings taken at right angles to the location of the grouse was used to determine position. The range of the directional antenna was approximately two km.

Once a Cessna 180 aircraft with a four element antenna attached to each wing strut was used to locate grouse (Anon. 1975). At an altitude of 320 m the maximum range a signal could be distinguished was about 12 km. By making several passes over an area at lower altitudes the location of a grouse was ascertained. Ground checks after the flight pinpointed the birds' positions.

Each grouse was located at least twice and up to four times daily on most days during the study. Locations were plotted on 6.13 cm to one km aerial photographs of the study area. These locations were used to determine home ranges and to relocate sites for habitat analysis. Home ranges were determined using the minimum home range method of Mohr (1947). Areas were calculated from air photos with a compensating polar planimeter. Minimum daily distances travelled equalled the distance in a straight line between daily locations (Robel et al. 1970). Where several locations were made in a day, the daily distances were the sum of the straight lines that connected all of these points (Godfrey 1975). Several times throughout the study individual females were monitored on an hourly basis from dawn-to-dusk to further elucidate daily movement patterns.

Habitat Use

Each location of a grouse, determined by radio telemetry, was assigned to one of eight habitat types based on descriptions by Pepper (1972) and Moyles (1977). These locations are also referred to as activity sites.

The habitat types are:

- 1) hayfield - sown to grasses and forbs such as alfalfa and sweet clover
- 2) grassland - dominated by native grasses and forbs
- 3) grass-shrub - a mixture of grasses, forbs and low shrubs (< 1 m), grasses and forbs form over 50% of the vegetative cover
- 4) shrub - dominated by low shrubs (< 1 m)
- 5) tall shrub - woody shrubs or saplings (> 1 m)
(sapling) but (< 3 m) high form over 50% of the cover at the site
- 6) open forest - trees (> 3 m) high are dominant, canopy closure (estimated) less than 30%
- 7) closed forest - dominated by trees, with a canopy cover (estimated) greater than 30%
- 8) marsh - dominated by wetland vegetation, standing water often present

A cover map using the above habitat types was constructed from a 1:60,000 true-color aerial photograph of the study area (Sexton and Dixon 1978). Home range maps in the text are plotted over portions of the cover map. The cover map was also used to determine habitat availability (Moyles, 1977).

In discussing habitat types with reference to instrumented female grouse, I refer to open and closed habitat or cover types. Open cover is that habitat with an open overstory and includes hayfields, grasslands, and grass-shrub areas. Closed cover refers to sites with closed overstory or canopy where branches touch. This generally includes shrub, tall shrub and forest habitat types. Marshes are not included in either class but are referred to directly.

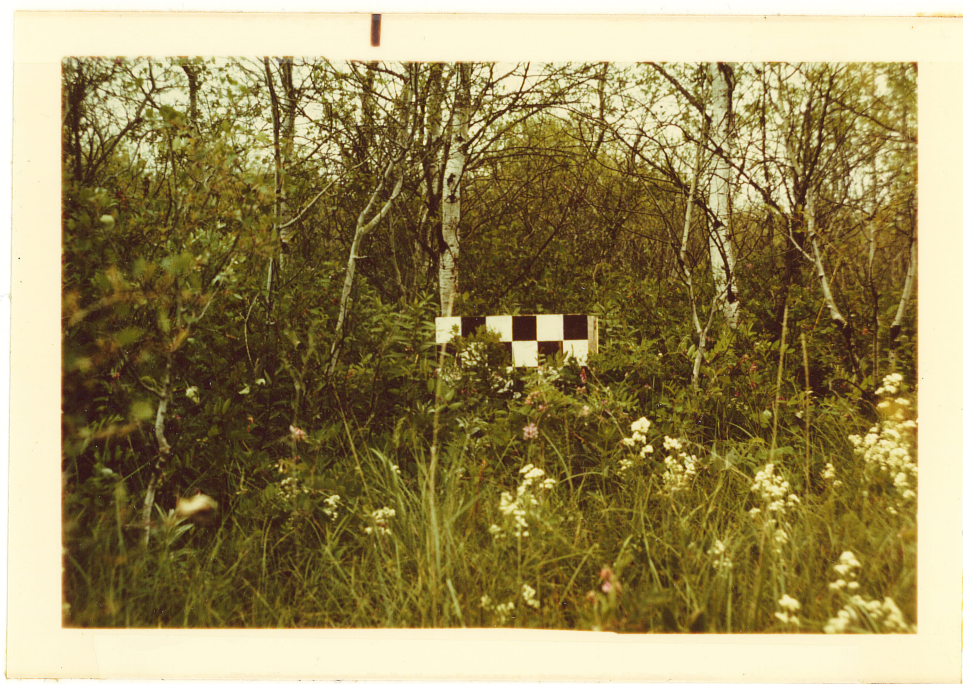
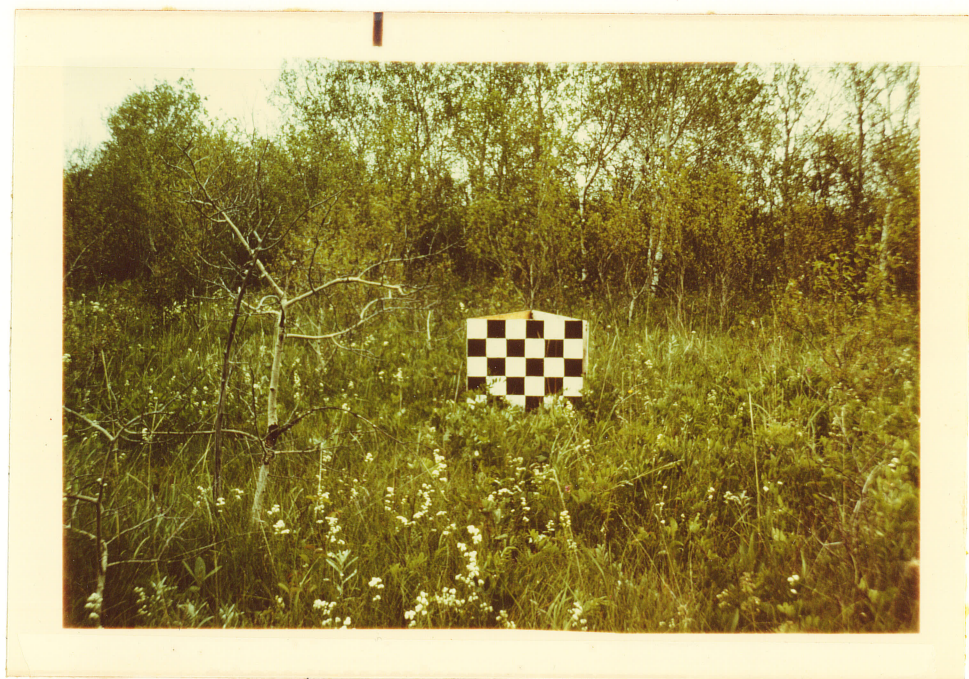
Habitat Analysis

Using a two-square meter quadrat placed at each activity site, frequency and density of shrub species were recorded. Also, frequency and Braun-Blanquet cover classes (Kershaw 1973) were determined for grasses, sedges and forbs at these sites. The latter were expressed as mean cover values for each species where the means were calculated only for sites with that species present.

During pre-incubation, five randomly placed quadrats in the same habitat type as the activity site were analysed the day following use of the site. At nest sites 15 randomly placed quadrats within 10 m of the nest were sampled as above. In addition, the average height of grass/forb, shrub, and residual strata were measured. The nest site exposure according to cardinal direction was determined. Nest sites and random plots around them were analysed the day after hatching. Post-nesting activity sites were analysed in a similar way, the day following use by grouse. (see also Appendix 2)

At all activity sites and nests a modified Jones (1968) cover board was used to quantify the vegetative cover. The board was 3-sided with each side gridded into 36 10 x 10 cm squares alternating black and white. Jones (1968) indicated that readings taken at "grouse eye level" gave the best comparative data for analysing activity sites. From 15 cm above the ground and 10 cm from the board I determined the percentage of squares obscured by vegetation at each site (Fig. 3). Random plots around each nest were also analysed in this way. Cover board and penetrated light values are dependent upon the combined structural components of sites analysed. They should be superior methods of determining habitat quality or for comparing microhabitats chosen at activity sites, based on studies by Jones (1968) and Weins (1969).

Figure 3. Cover board used in an open area (above)
and closed cover area (below).



At all activity sites the percent light penetration was determined using a Gossen Tri-Lux foot candle meter modified from Keith (1961) and Weins (1969). Two readings were taken 15 cm above ground level, and above the vegetation canopy at the site or in the open nearby. The two values were averaged for each and a ratio of the site to the exposed reading calculated. This percentage value indicated the amount of light that penetrated the vegetation canopy at the site.

At brood locations the site and ambient ground temperature were recorded whenever possible. Ambient ground temperatures were obtained with a mercury thermometer 10 cm above the substrate in an open (sparsely vegetated) site, shading it and recording the temperature after about five minutes. Site temperature was recorded in the same fashion at the activity site. These temperatures were recorded only when the precise location (within 0.5 m) was known, such as when broods were flushed. The temperature readings were then taken immediately.

Field Observations

Direct observations of instrumented birds were made only occasionally. The birds were seldom disturbed during tracking and monitoring. Nests were visited once or twice during incubation to determine clutch size. Nest attentiveness, periods away from nests, and locations of birds at these times were determined by monitoring females

at least 50 m from nest sites. The incubation period was recorded for most nests that hatched successfully. I ascertained, where possible, the predators of nests that were destroyed and grouse preyed upon using descriptions in Einarsen (1956).

Brood size was noted for all broods flushed in the study area. Flush sites were searched carefully to insure that all young were counted. Locations of unmarked broods were plotted on air photos to determine their positions in relation to instrumented grouse.

All times are reported as central daylight time.

Statistical Tests

Statistical tests follow Sokal and Rohlf (1969) or Siegal (1956). Level of significance in all tests is 0.05 level of probability, unless stated otherwise. Means are expressed as \pm one standard error.

RESULTS

Pre-incubation

Home Range and Movements

Nineteen female Sharp-tailed Grouse captured at arenas were equipped with transmitters and tracked prior to incubation. Eleven of these provided complete information on home ranges in the pre-egg and egg stages. Two others permitted ranges in the pre-egg stage to be calculated. Daily distances moved and habitat types used were determined for all grouse monitored.

Female grouse tracked after they left arenas when released showed two types of behaviour and were assigned to one of two groups.

- I Females that remained within one km of the capture arena and did not visit other arenas.
- II Females that moved more than one km from the capture arena and/or visited other arenas.

There was a significant difference in the mean daily distance moved by these groups in the pre-egg stage (Table 1). Group II females moved farther each day, beginning immediately after release. One female did not begin movements away from the capture arena until four days after being released. Movements during this stage were achieved

Table 1. Mean daily distance (m) moved by females during pre-incubation.

Females	Pre-egg ¹	Egg ²
Group I	277.6 (9) ³	98.3 (6)
Group II	350.0 (4)	107.2 (3)

¹Mann Whitney $U_{4,9} = 3$ $P < 0.05$

²Mann Whitney $U_{6,3} = 10$ $P > 0.05$

³Number of females tracked

by a combination of walking and flight based on observations of marked and unmarked birds. Group II females were never observed on or within 25 m of a capture arena after release whereas Group I females were often seen on or near their respective capture arenas. One female was seen on the arena 18 days after she was captured there, and three days after she deserted her nest. Two other females were located several days after their release on the edge of their capture arenas, but did not go onto the arenas while I was watching.

Pre-egg home range size was significantly larger in Group II females (Table 2). Their mean home range was more than twice as large as Group I birds. Pre-egg home ranges were elongate in both groups. Furthermore, the length:width ratio for Group II birds was almost twice that of Group I females (4.43:2.67, respectively).

The existence of two groups of females is reinforced by the pre-egg and egg ranges of female 4109, a Group I female (Fig. 4). Her original pre-egg home range was adjacent to arena 3 but her nest was destroyed by an unknown predator early in the egg stage. Her second pre-egg range included much of the first and was also around arena 3. She was in the vicinity of her first nest (within 5 m) at least twice. Her second was located 290 m from her first nest.

Table 2. Mean area (ha) of home ranges during pre-egg and egg stages.

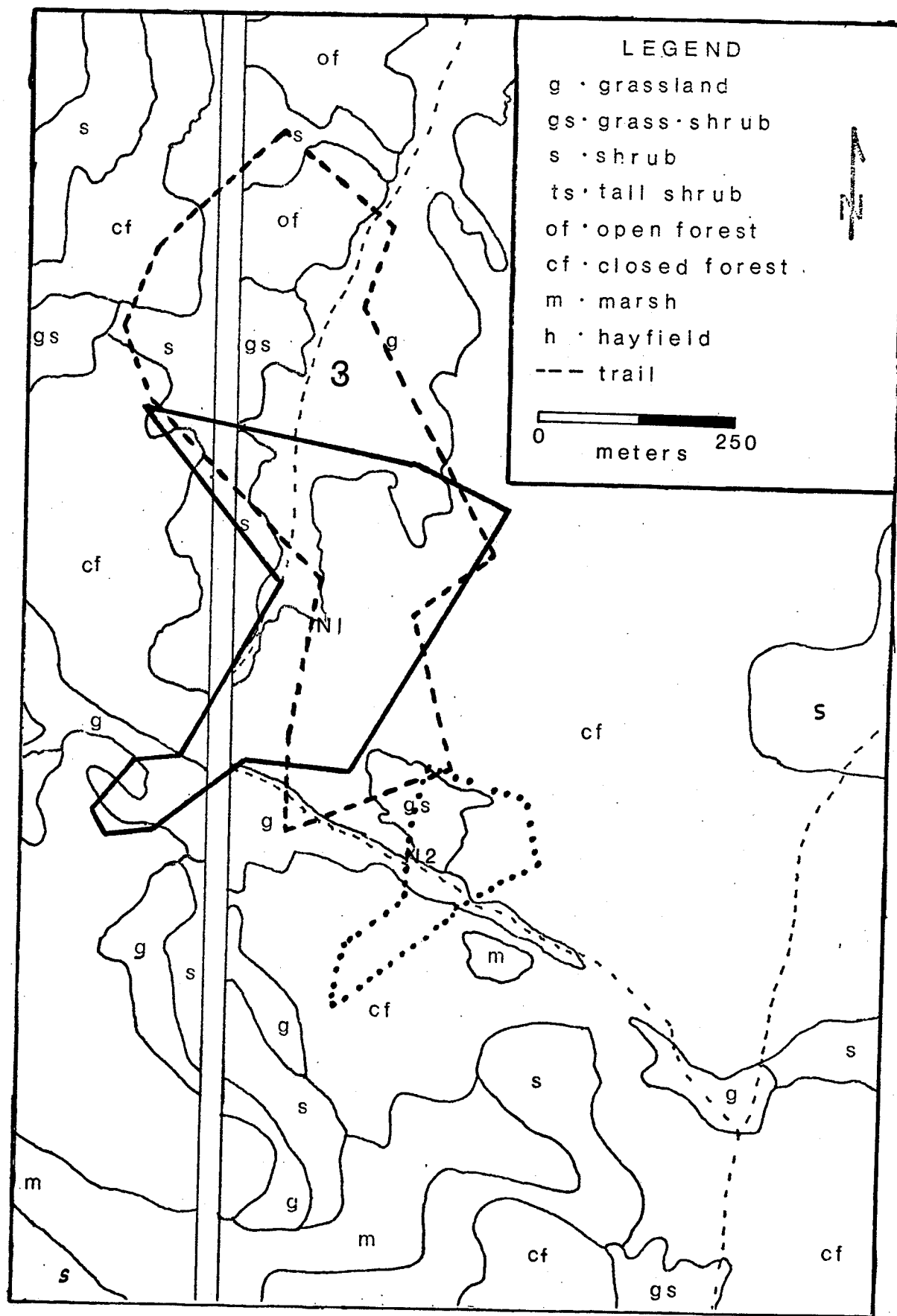
Females	Pre-egg ¹ (\pm SE)	Egg ²
Group I	12.54 \pm 5.94 (9) ³	2.79 \pm 0.19 (6)
Group II	33.71 \pm 10.10 (4)	3.51 \pm 0.96 (3)

¹Mann Whitney $U_{4,9} = 0$ $P < 0.05$

²Mann Whitney $U_{6,3} = 6$ $P > 0.05$

³Number of females tracked

Figure 4. Pre-egg ranges prior to first nest (solid line), renest (broken line) and egg home range (dotted line) of renest for female 4109. N_1 and N_2 show location of first nest and renest, and "3" denotes location of arena 3.



Group II females were sometimes located at more than one arena during the pre-egg stage. Female 4101, instrumented on arena 3, was located three times during a four day period along the edge of the field in which arena 5 was located (Fig. 5). In one case males were actively displaying at the time of the location and the female was less than 20 m from the arena. Another female (1-8.4) was tracked to a site within 50 m of an arena in late morning although males were no longer there.

Predation on Group II females was greater than on Group I females during the pre-incubation period, although the difference was not statistically significant (Table 3). Although avian predators were responsible for most females killed during this period, one bird was probably killed by a coyote.

Movements during the egg-laying stage were restricted in both groups. There was no significant difference in minimum daily distance moved by the females in the two groups (Table 1). During this stage females were relatively sedentary from mid-morning until late afternoon. Movements usually occurred before 10:00 hr and in the evening before dusk.

There was no significant difference in home range size of the two groups during egg-laying (Table 2). The length:width ratios were similar (2.20 Group I:1.74 Group II) and suggest a more circular home range during this stage. Egg-laying home ranges were usually at least

Figure 5. Movements of female 4101 between
27 April and 11 May 1977. Arenas 3
and 5 are denoted by "3" and "5".

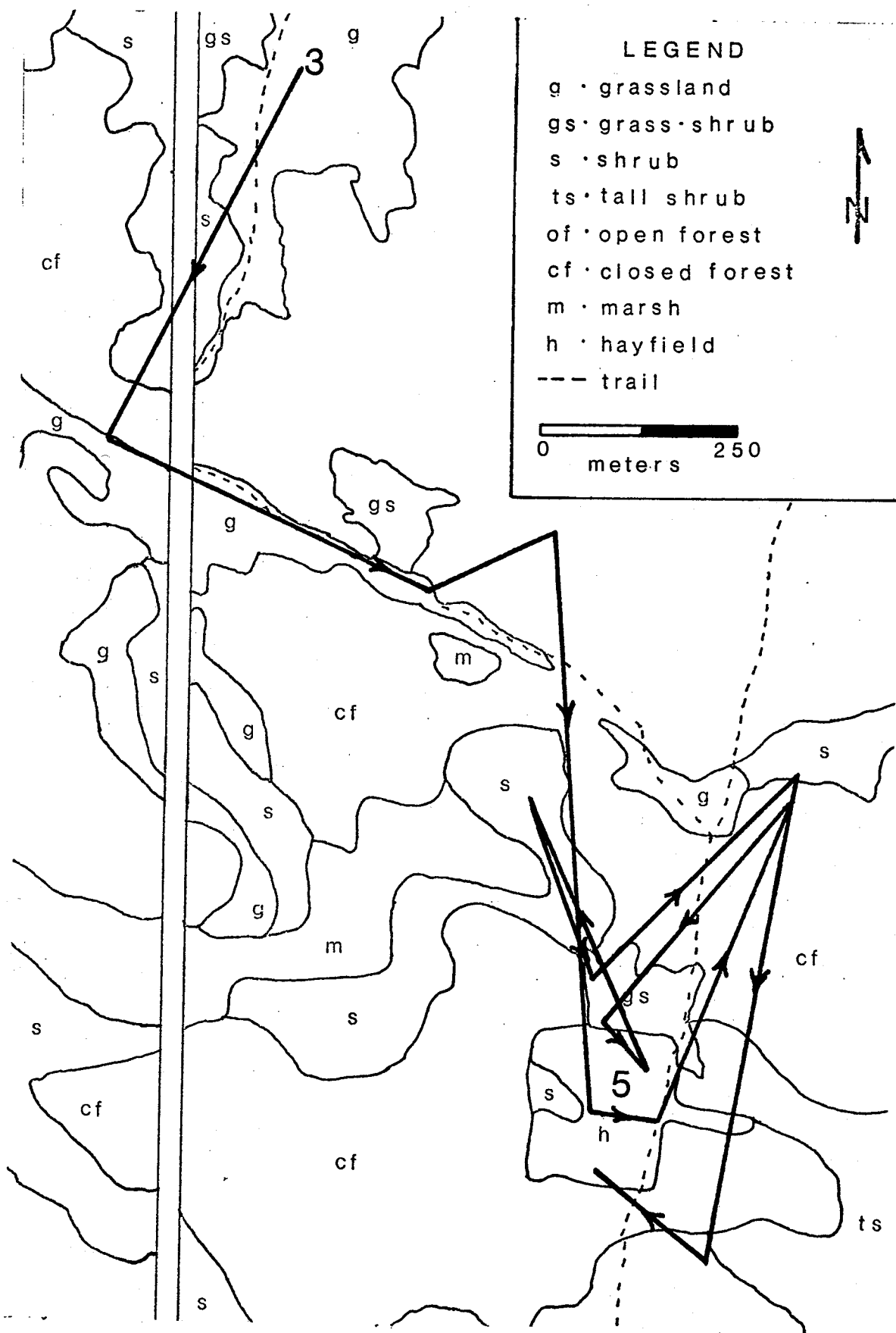


Table 3. Predation on Group I and Group II females during pre-incubation.

Females	Survived to Incubation	Were Preyed Upon
Group I	7	2
Group II	4	4

Fisher Exact Probability Test, $P > 0.05$

partly contained within the pre-egg range. The female with the smallest egg-laying range (2.2 ha) was a Group II female. Her range was centered around a small open patch of grass-shrub less than 2 ha, in a predominately forested area. The largest egg-laying range (4.8 ha) was of a renesting female and was situated in an area of scattered clumps of shrub and trees in a grass-shrub area.

Only once was a female located at her nest during the egg-laying period. After laying she walked away from the nest and spent the rest of the day 100 m or more from the site, as was typical of most females. Nest sites were most often along one edge rather than centrally located in the egg-laying home range.

Home Range Overlap and Association with Conspecifics

Female 4107 was located twice on the same day within the eastern limit of female 4109's home range during the pre-egg stage (Fig. 6). Female 4107 was not located again in this area of overlap. Female 4109 continued to use the area and eventually nested immediately adjacent to it. The closest these birds were located together by tracking was approximately 100 m on 28 April 1977.

After 4109's first nest was destroyed she was located three times on 20 May within the egg-laying range of female 4107 (Fig. 7). At this time female 4107 was incubating. One of three locations was within 60 m of 4107

Figure 6. Pre-egg home range of females 4107
(solid line) and 4109 (broken line).
Hatched portion is area of overlap
and "3" denotes location of arena 3.

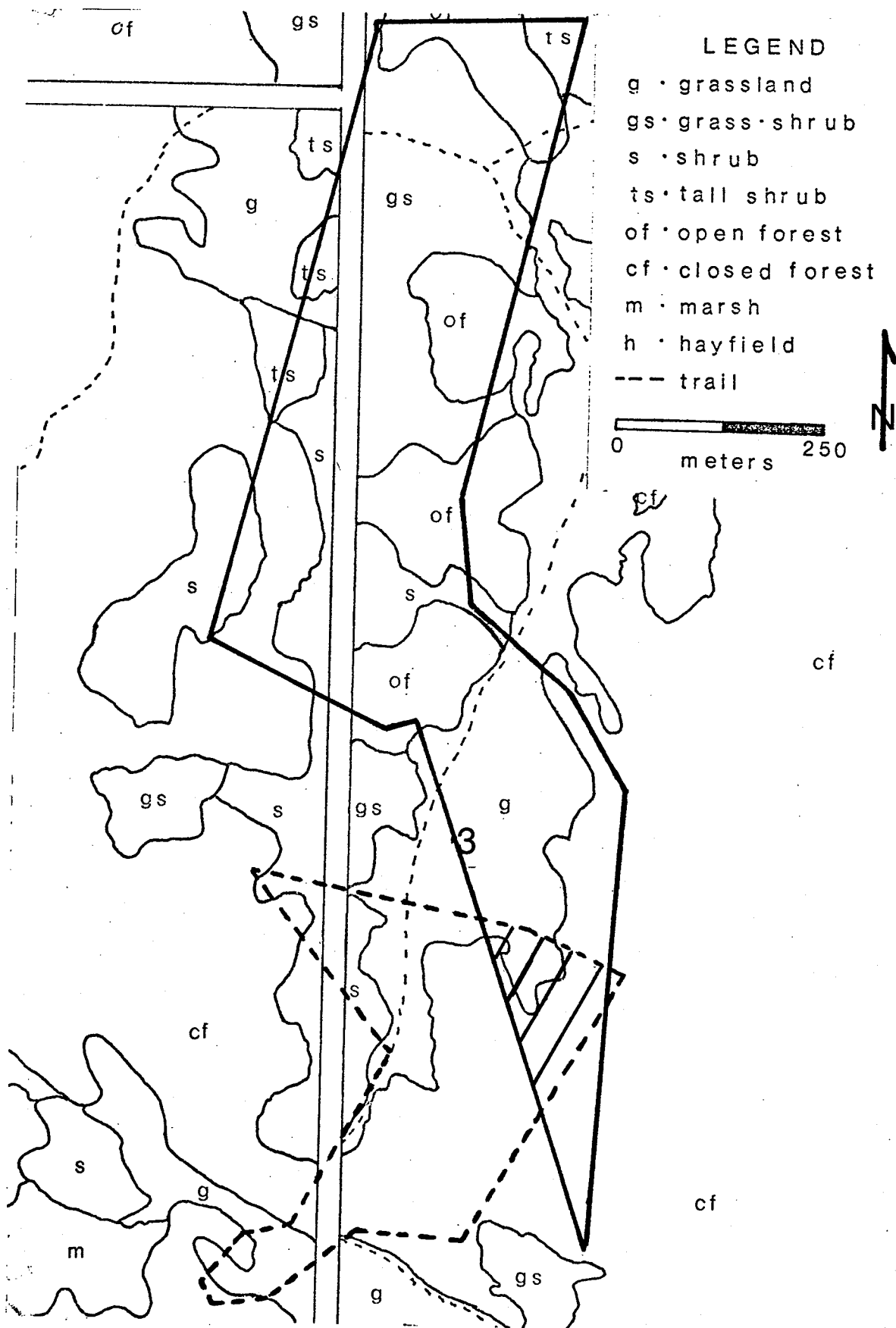
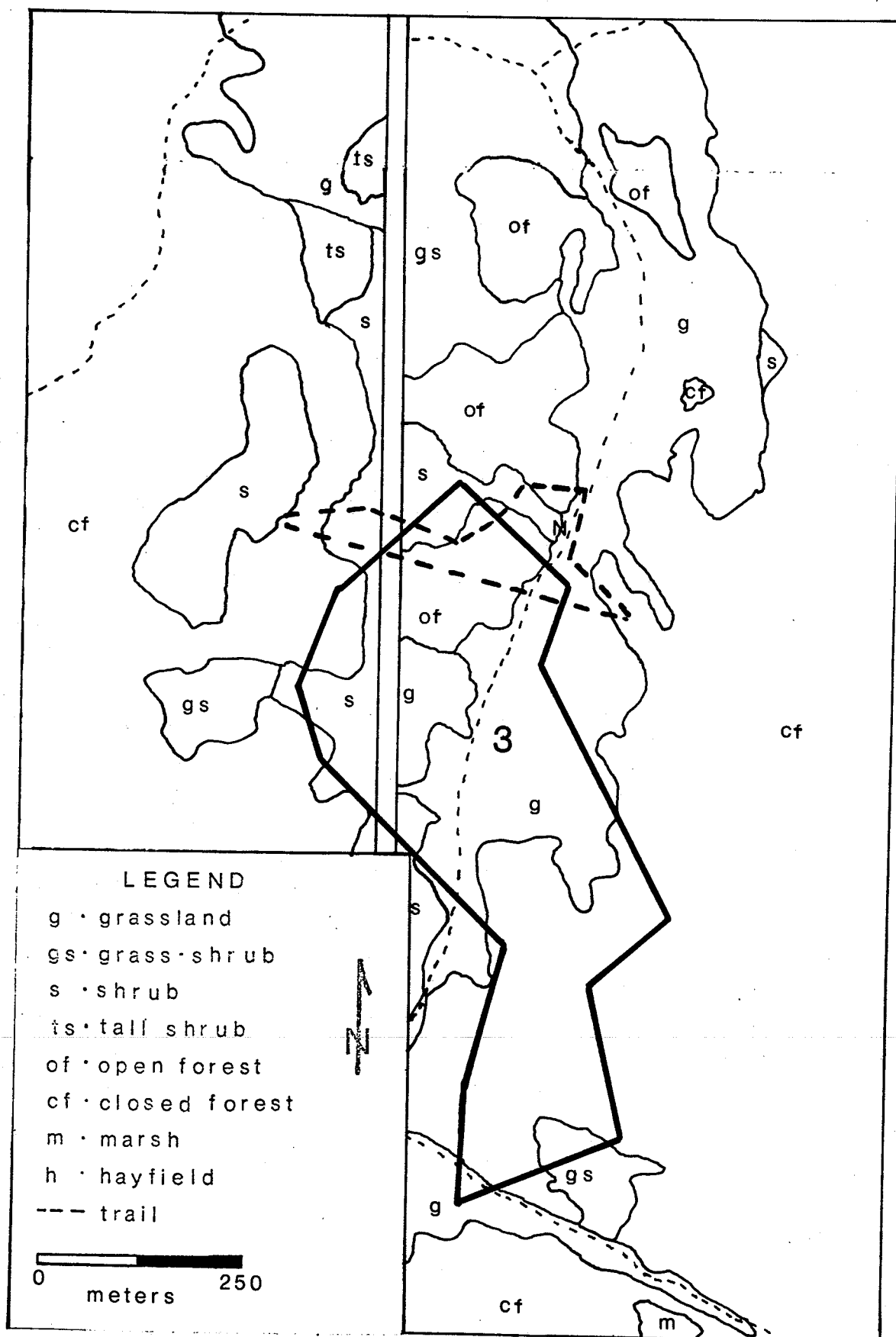


Figure 7. Pre-egg home range (renest) of female 4109 (solid line) and egg-laying home range of female 4107 (broken line). N_1 is location of nest of female 4107 and "3" denotes arena 3.



35

(on nest). These observations occurred four days after the destruction of 4109's first nest. Female 4109 was not located in the above overlap area after 20 May.

Female 4109 and 6484 were within 30 m of each other on 8 May 1977. Female 6484 had just been instrumented about 24 hours previously on arena 3. The day following the close contact female 6484 was located 350 m west of the above nest whereas female 4109 was less than 100 m from this site. Female 6484 was subsequently classed as a Group II bird based on her movements.

Close contact was recorded once during the egg stage. I flushed an unmarked Sharp-tailed Grouse (sex unknown) about 35-40 m from the site of an instrumented female I had just tracked. The marked female was about midway through the egg-laying stage.

From observations away from arenas Group II females were seen significantly more often with conspecifics than Group I birds (Table 4). Group II females were seen with more than one other conspecific on three of eight occasions whereas Group I females were never seen with more than one Sharp-tailed Grouse. All of these observations occurred during the pre-egg stage.

Table 4. Locations of females with conspecifics during pre-incubation.

Females	Locations	
	Alone	With Conspecifics
Group I	22	4
Group II	10	8

$$\chi^2 = 5.795, 1 \text{ d.f.}, P < 0.05$$

Pre-incubation Habitat Use

There was no significant difference ($\chi^2 = 2.60$, 4 d.f., $P > 0.05$) in habitat types used by females during the pre-incubation period when the two study years were compared. Table 5 shows that habitat types used during the pre-egg and egg stages were significantly different. There was a significant correlation ($r = 0.98$, 2 d.f., $P < 0.05$) between decreasing use of forest habitat and the approach of incubation. That is, as spring progresses forest habitat is used less. There was no concurrent significant increase in use of any other one habitat although shrub was used slightly more.

Group I and II females used similar habitat during the pre-incubation period (Table 6). A Group II female whose home range was confined to a forested area used open glades (sometimes 100 m apart) and their peripheries during much of the pre-egg stage. I suspect she flew from one opening to another as locations were never more than 20 m from the opening into the forest. Similarly, females located in forest habitat during this period were never more than 25-30 m from some open habitat such as grass or grass-shrub.

There was no significant difference in habitat types used by females killed, prior to their death, and those that were not preyed upon (Table 7). Kills were not restricted to a particular habitat type and were not found more often in either open or closed cover.

Table 5. Habitat types used by females during pre-incubation.

Habitat Type	Number of Locations			
	Pre-egg	(%)	Egg	(%)
Grassland	5	(5)	6	(10)
Grass-shrub	16	(14)	18	(30)
Shrub	17	(15)	8	(13)
Sapling	7	(6)	5	(8)
Forest (open and closed combined)	65	(60)	24	(39)
Total	110		61	

$$\chi^2 = 11.03, 4 \text{ d.f.}, P < 0.05$$

Table 6. Habitat types used by Group I and Group II females during pre-incubation.

Habitat Type	Locations	
	Group I	Group II
Grass	6	5
Grass-shrub	21	12
Shrub	17	8
Sapling	6	6
Forest (open and closed combined)	39	51
Total	89	82

$$\chi^2 = 7.11, 4 \text{ d.f.}, P > 0.05$$

Table 7. Habitat types used by females during pre-incubation in relation to survival.

Habitat Type	<u>Locations According to Survival</u>	
	Preyed Upon	Survived
Grass	5 ¹	6
Grass-shrub	13	20
Shrub	8	17
Sapling	5	7
Forest	26	64
Total	57	114

¹Number of locations

$\chi^2 = 2.46, 4 \text{ d.f.}, P > 0.05$

Grasslands and open forest were used in relation to availability whereas grass-shrub and shrub were used more often and closed forest marsh and sapling less (Table 8).

Females made greatest use of open habitats (grass and grass-shrub) during morning and evening (Fig. 8). From mid-morning to late afternoon habitat types with a greater proportion of woody species were used. Over 70% of locations at this time were in shrub, sapling or forest habitats. Night roosts were most often in small clumps of dense shrub surrounded by open grass or grass-shrub cover, although openings in forests were used occasionally.

Cover board values (Table 9) obtained during the day indicate there is a significant difference ($F_{7,46} = 2.79, P < 0.05$) in cover used. There was also a significant difference ($F_{7,58} = 4.42, P < 0.05$) in penetrated light. Table 9 indicates that sites with less penetrated light are used during mid-day and more open sites are used in morning and evening.

Species of ground plants most frequently found at activity sites are listed in Table 10. Residual grass was present at all sites and was the major element of the ground cover at these sites. Early spring perennials (Galium, Fragaria, Thalictrum, Taraxacum) as well as grasses comprised most of the ground cover present. Woody species most frequently found at sites are presented in

Table 8. Habitat types used by females during pre-incubation in relation to habitat availability.

Habitat Type	Used ¹ (%)	Available	X ²	Significance Level
Hayland	0.0	2.5	6.63	0.02
Grassland	6.4	4.9	1.36	n.s.
Grass-shrub	19.3	12.0	12.59	0.001
Shrub	14.6	8.0	15.49	0.001
Sapling	7.0	12.0	6.26	0.02
Open forest	46.2	42.2	0.02	n.s.
Closed forest	6.4	13.5	10.39	0.01
Marsh	0.0	4.7	13.15	0.001

¹n = 171 locations



Figure 8. Within "day" use of habitat types by
females during pre-incubation.
(n = 171 locations)

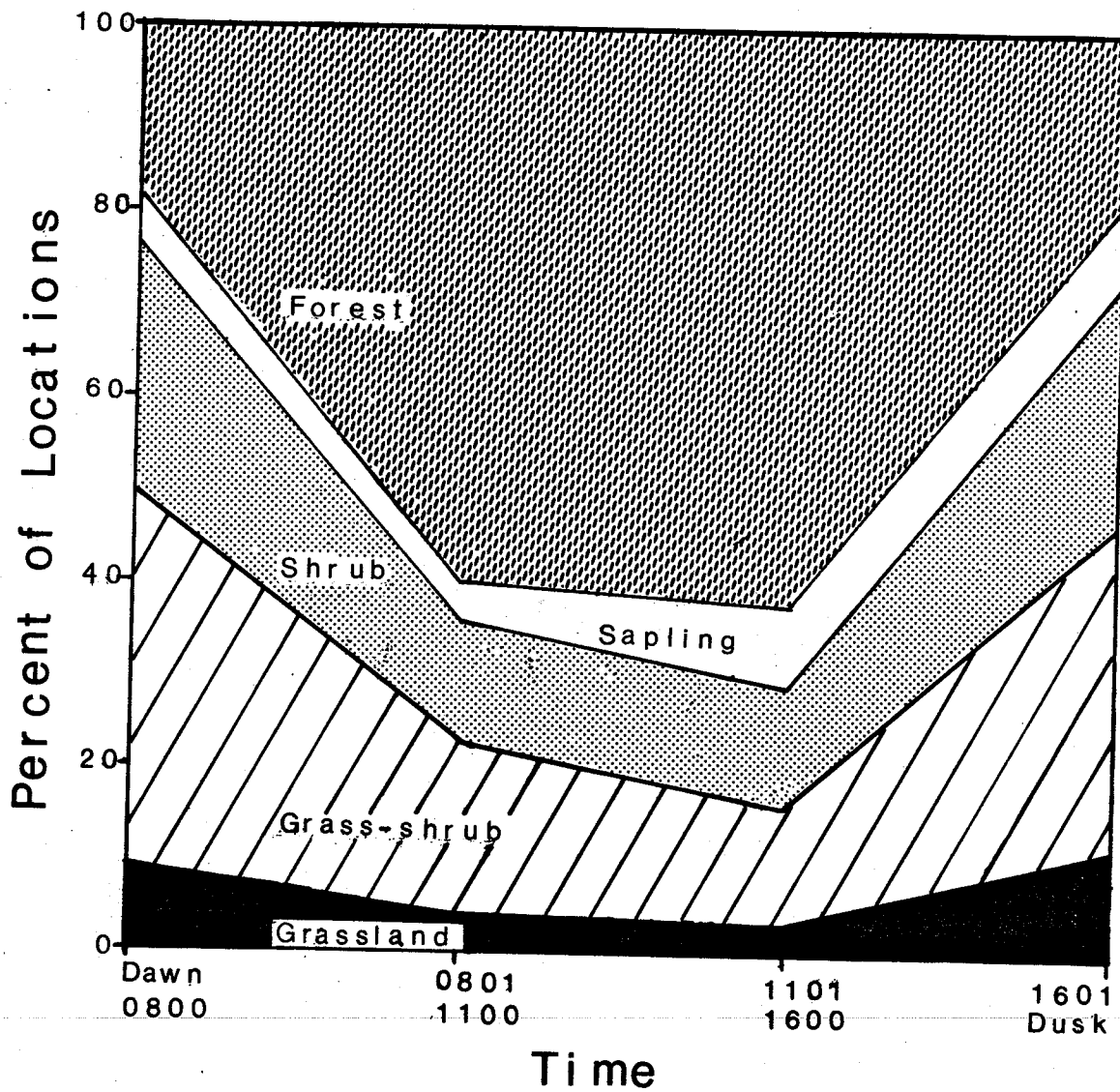


Table 9. Cover and penetrated light values at
activity sites of females during pre-incubation.

Time Interval	Mean Percent Cover Board (\pm S.E.)	Mean Percent Penetrated Light
<0800	59.8 \pm 9.3 (8) ¹	89.9 \pm 8.4 (9)
0801-1100	65.8 \pm 5.4 (11)	63.7 \pm 6.2 (11)
1101-1600	53.8 \pm 7.2 (21)	60.2 \pm 9.6 (21)
1601-dusk	58.2 \pm 5.0 (23)	78.1 \pm 6.4 (28)

¹Number of locations

Table 10. Frequency and cover rating of grasses and forbs
at activity sites of females during pre-incubation.

Species	Percent Frequency of Occurrence	Total Cover Rating ¹
Gramineae (residual)	100	329
<u>Fragaria</u> spp.	46	63
Gramineae (current)	40	53
<u>Galium boreale</u>	26	30
<u>Carex</u> spp.	18	18
<u>Pyrola</u> spp.	12	6
<u>Taraxacum officianale</u>	11	21
<u>Lathyrus</u> spp.	9	6
<u>Thalictrum</u> spp.	7	24
<u>Solidago</u> spp.	7	5
Compositae	4	1

¹Braun-Blanquet cover rating

Table 11. Shrubs typically found include Populus, Rosa, and Amelanchier whereas species common to lowland sites (Salix, Cornus, Betula) occur less frequently. When species composition of sites and sample plots are compared, lowland shrubs are present more often in sample plots than at sites (Table 11). Shrubs found in dry, upland sites (Symphoricarpos, Arctostaphylos) are common at activity sites.

Use of Burned Areas

A fire in early April, 1977, burned much of the ground cover in the western part of the study area. It eliminated residual grass and forb cover, especially on upland sites. Shrubs and trees were usually slightly affected, but in a few sites stands of Populus saplings were thinned appreciably by the fire.

The area affected by the fire was used by females during the pre-egg and egg stages. Female 4107 was located there twice on 2 May and once each on 15 and 16 May. On 2 May she was in an open area with little ground cover. The site was less than 10 m from an unburned lowland area into which she flew after I flushed her. She was back in this open area about six hours later. On 15 May this female was located along the edge of a patch of shrub that had some unburned residual cover present. By this time there was some of the present year's growth in the burned area. The next day she was about 120 m

Table 11. Frequency of shrubs at 91 activity sites
and 225 sample plots during pre-incubation.

Species	Frequency			
	Activity Sites (%)		Sample Plots (%)	
<u>Populus tremuloides</u>	86	(95)	203	(80)
<u>Rosa</u> spp.	32	(35)	94	(37)
<u>Amelanchier alnifolia</u>	28	(31)	97	(38)
<u>Symphoricarpos occidentalis</u>	25	(27)	41	(16)
<u>Betula glandulosa</u>	16	(18)	61	(24)
<u>Arctostaphylos uva-ursi</u>	15	(17)	23	(9)
<u>Salix</u> spp.	14	(15)	74	(29)
<u>Potentilla fruticosa</u>	6	(6)	18	(7)
<u>Corylus cornuta</u>	5	(5)	5	(2)
<u>Cornus stolonifera</u>	2	(2)	10	(4)

from the previous site in an unburned forested area within the burned portion of the study area. She had left the burned area eight hours later.

Female 4109 also spent considerable time in the burned area (2-5 May, 9-11 May, 20-21 May). Her activities were centered around patches of dense Betula during the first two periods and a partly burned forested area for the latter. Small patches of residual cover were present in all of the lowland areas that were missed by the fire.

Incubation

Nests

Fourteen nests were found by tracking instrumented female Sharp-tailed Grouse (Fig. 9). Twelve were within 1 km of an arena and 11 were within 1 km of the arena on which the female was captured (Table 12). The clutches in seven of the nests hatched successfully, five were preyed upon by mammals and two were abandoned.

Clutch size averaged 11.6 eggs for all nests (range 9-15) and 12.1 for first nests. Two renests were located with clutches of nine and 10 eggs. Hatching success of nests producing young was 91%. At one nest only five of ten eggs laid hatched. For all nests 72 eggs of 128 laid (56%) hatched.

Figure 9. Distribution of nests. Lines connect nests and capture arenas.

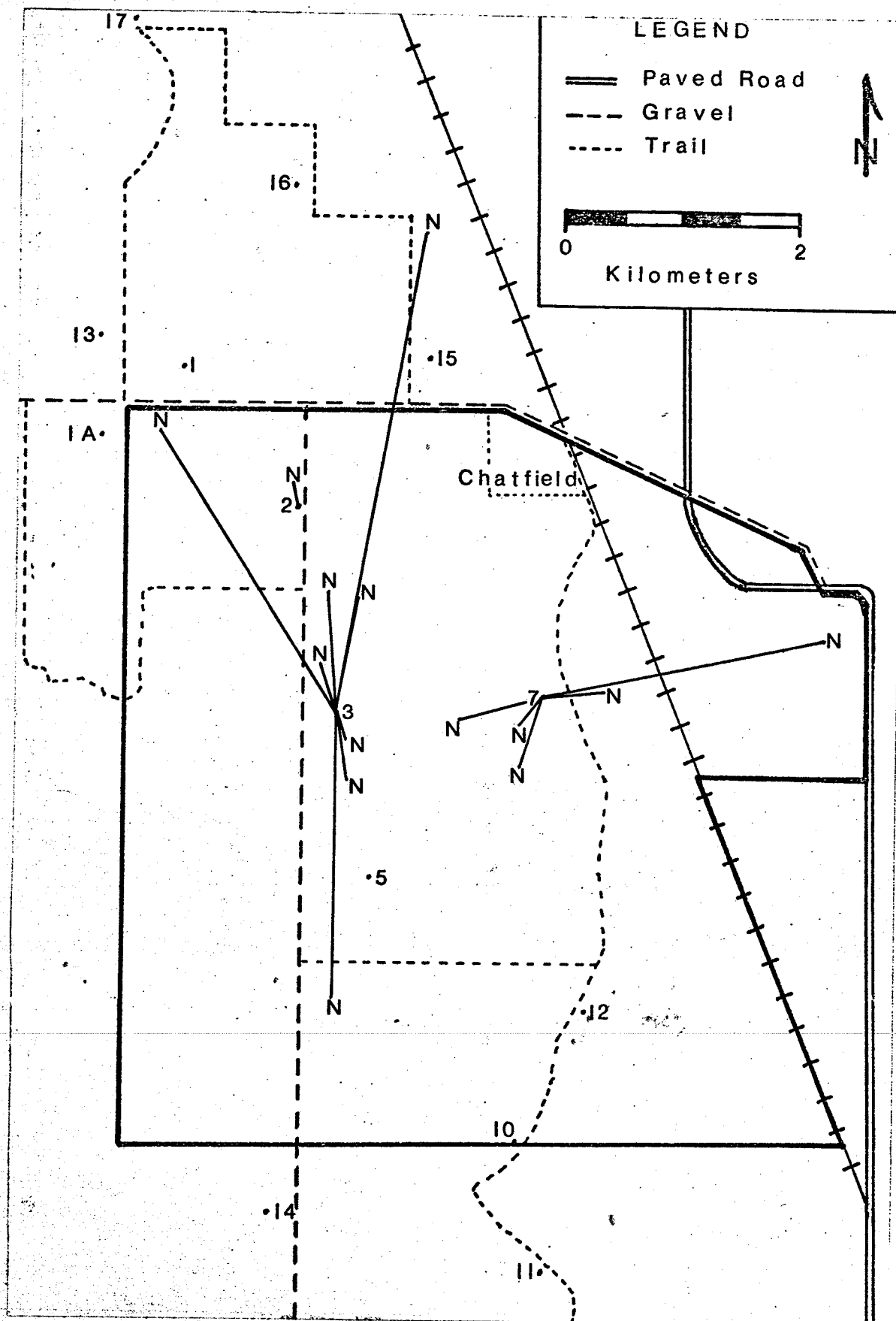


Table 12. Distance from arenas to nest sites.

Nests	Distance to arena (km)			
	0.0-0.5	0.51-1.0	1.01-1.5	>1.5
In distance range to nearest arena	6	6	1	1
In distance range to capture arena	6	5	0	3

One instrumented female provided information on the rate of egg laying. She was located at 18:07 hr on 2 June 1977 in an area of grass-shrub habitat. By 18:40 hr she had left the area by walking. A search of the earlier site revealed a nest containing six eggs. This bird was not located at or nearer than 60 m to the nest during the subsequent tracking intervals until 16:45 hr on 6 June 1977. Direct observation of the nest indicated she left the eggs uncovered during her absence between laying eggs. Seven eggs were present in the nest at 19:51 hr on 3 June 1977. The complete clutch contained 9 eggs. This suggests the last two eggs were laid over a three day period. Incubation periods obtained from four nests were 23, 23, 23, and 24 days.

Nest Site Vegetation

Eleven of the 14 nests were in grass-shrub habitat and three were in small grassy openings in open forest. Eleven nests had a northern exposure (Table 13). Grasses, Populus and Amelanchier occurred most often at nests and in sample plots (Tables 14 and 15). The frequency of occurrence of most shrub, grass and forb species was similar at nests and sample plots around nests.

Populus, Amelanchier and Symphoricarpos provided most of the shrub cover at nests. Native grasses and Galium formed most of the herbaceous cover. None of the

Table 13. Orientation of Nests.

Direction of exposure	Number of ¹ nests
North	11
South	3

¹Binomial test $P = 0.029$

Table 14. Shrub composition and density at nests
and sample plots.

Species	% Frequency ¹		Density (/m ²)	
	Nest (14)	Plot (51)	Nest (14)	Plot (51)
<u>Populus tremuloides</u>	93	65	8.8	7.5
<u>Amelanchier alnifolia</u>	86	76	9.6	8.6
<u>Symphoricarpos occidentalis</u>	50	48	5.1	5.6
<u>Rosa</u> spp.	43	56	1.2	1.2
<u>Arctostaphylos uva-ursi</u>	36	25	-	-
<u>Potentilla fruticosa</u>	21	9	1.6	2.2
<u>Salix</u> spp.	14	17	1.6	0.9
<u>Betula glandulosa</u>	7	11	1.9	1.7

¹Species with a frequency of <10% in both columns omitted.

Table 15. Grass and forb composition and cover-rating
at nests and sample plots.

Species	% Frequency ¹		Mean Cover-rating ²	
	Nest (14)	Plot (51)	Nest (14)	Plot (51)
Gramineae	100	100	1.71	1.68
<u>Carex</u> spp.	14	12	1.00	1.67
<u>Galium boreale</u>	64	83	2.46	1.44
<u>Lathyrus</u> spp.	36	41	2.30	1.24
<u>Thalictrum</u> spp.	28	47	1.00	1.18
<u>Solidago</u> spp.	21	20	1.67	2.01
<u>Vicia</u> spp.	14	20	1.50	1.10
<u>Achillea</u> spp.	14	14	0.50	0.40
<u>Fragaria</u> spp.	7	14	1.00	0.78

¹Species with frequencies <10% in both columns omitted.

²Mean cover rating : total cover rating/plots, where species occur.

1.
nests was in stands of pure vegetation (such as Medicago fields). All were in a heterogenous mixture of shrubs, grasses and forbs.

Density of woody stems , the sum of stems of all species, was significantly greater at nest sites (Table 16). The mean height of shrubs was also significantly greater. All but one nest was located at the base of a shrub. Height of the current grass and forb growth was not significantly different at nest sites compared to plots. Residual grass/forb height was not significantly different either. Current growth of grass and forbs were very sparse when nests were initiated, throughout the study area. Residual cover was variable. Some areas had an abundance of grass and forb growth from the previous year whereas other sites had only scattered patches or very sparse residual cover. Residual grass cover was not present at all nests whereas grass formed the major component of residual cover in general in the study area.

Cover board values were not significantly different when nest sites were compared to sample plots. However, when nests were compared to sample plots within five meters of the nest, nest sites had significantly greater ($t = 2.08, 30 \text{ d.f.}, P < 0.05$) values than plots. Penetrated light values were significantly lower hence less light penetrated cover or it provided greater overall cover at nests. Figure 10 shows the marked difference in percent penetrated light at nests and plots within 10 m of the nest.

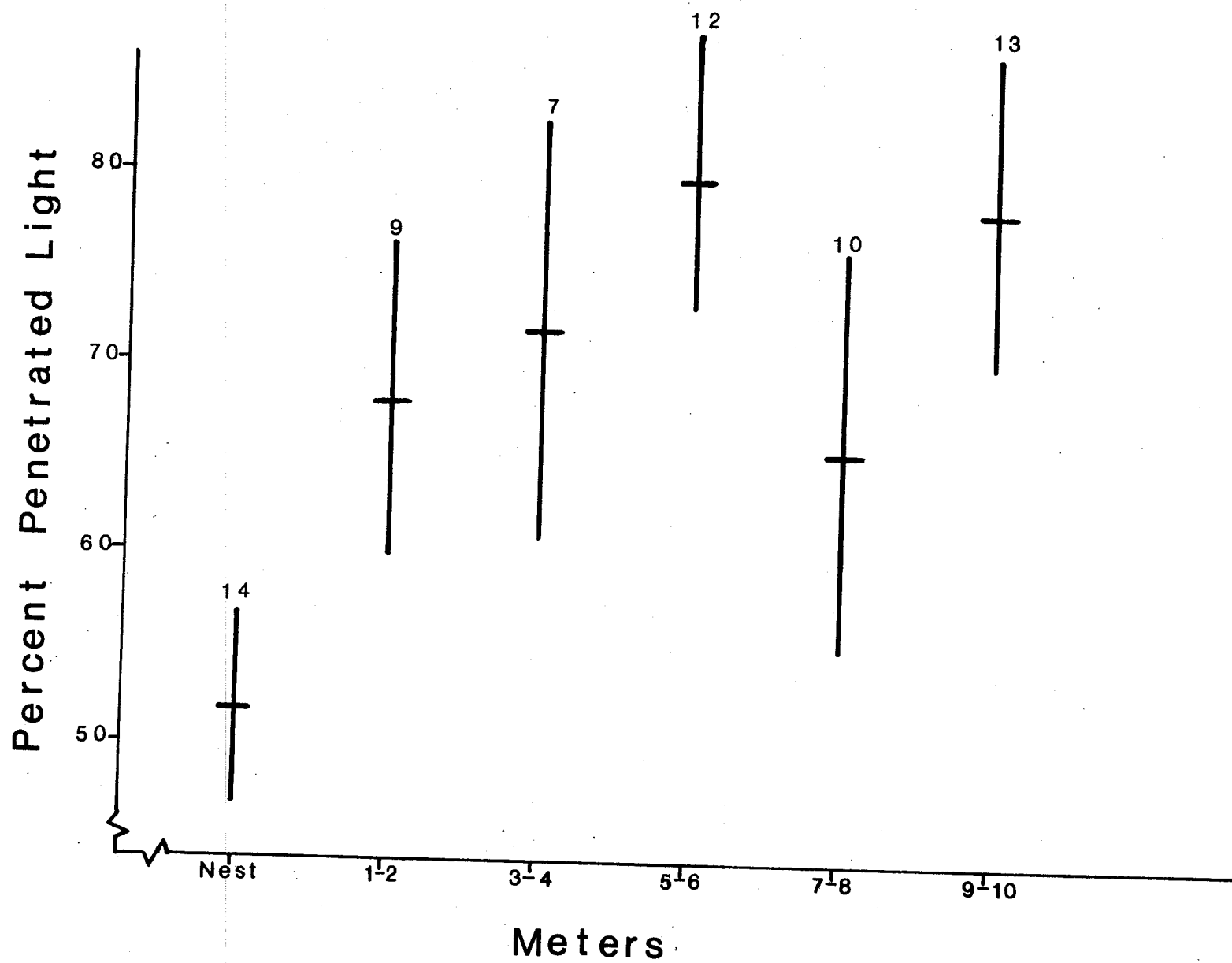
Table 16. Comparison of vegetation characteristics between nest sites and sample plots.

Characteristics	Nest ¹ (14)	Sample Site ¹ (51)	"t" value	Significance Level
Woody stem density (stems/m ²)	27.9 ²	19.5	3.06	0.001
Height of woody stems (cm)	75.8	55.2	2.89	0.005
Residual cover height (cm)	7.5	6.5	1.50	n.s.
Current grass/forb (cm)	26.4	23.9	1.10	n.s.
Cover board value (%)	76.0	68.8	1.29	n.s.
Penetrated light (%)	51.1	64.3	2.64	0.005

¹Sample size

²Entries in table are means of each category.

Figure 10. Percent penetrated light of vegetation at different distances from nests. Horizontal line is the mean, the vertical bar is 95% C.I. Sample size is above vertical bar.



All nests were located close to dense shrub or forest habitat. Most nests were located within 20 m of the nearest dense woody cover (Table 17).

All incubating females were flushed from nests at least once, and some up to three times. On 27 occasions when females were flushed, they flew to and landed in the nearest dense cover over 70% of the time (Table 18).

Movements of Incubating Females

Attentiveness of incubating females is shown in Table 19. Females were located off the nest only 10% of the time, based on 219 radio checks of incubating birds. At over half the locations away from the nest the birds were in close proximity to it but never moving. Of locations made of females away from the nest all but one took place in the evening. Five of the locations of females near the nest were made between 10:00 hr and 16:00 hr and occurred on overcast or rainy days. Females did not cover the eggs with nesting material or litter during their absences.

Females tracked to sites away from nests were located in grass or grass-shrub cover on eight of the 12 occasions. The other locations were made along forest edges or in stands of dense shrub. Mean distance from nests to the 12 sites was 98.6 m (range 45-100 m).

Table 17. Locations of nests relative to forest
or shrub cover.

Number of Nests	Distance from Nest (m)		
	0-10.0	10.0-20.0	>20.0
From nearest cover	10	4	0
From next nearest cover	5	8	1

Table 18. Use of forest or shrub cover by females
flushed from nests.

Proximity of cover in relation to nest	Cover flown to when flushed (%)	
Nearest	19	(70)
Next Nearest	5	(19)
Other	3	(11)
Total	27	

$$\chi^2 = 16.29, 1 \text{ d.f.}, P < 0.05$$

Table 19. Locations of females when monitored during incubation.

Year	Relation to Nest		
	On	Near (<5m)	Away (>5m)
1976	68	6	5
1977	<u>129</u>	<u>4</u>	<u>7</u>
Total	197	10	12

Female 6489 was observed 3 times feeding on ground vegetation, either grasses or forbs in a grassland area about 100 m from her nest. A check of the site after she left did not reveal a preponderance of any one type or species of vegetation that she may have been selecting. Once I saw this female returning to her nest after feeding. She flew from the feeding site and landed approximately 10 m from the nest. A check ten minutes later, using the radio receiver, indicated she had walked the remaining distance to the nest.

Female 6486B was observed feeding on ground vegetation in a grassland area 115 m from her nest. Two days later she was accidentally flushed from a site about 10 m from the location described previously, but still within the same grassland area. A check of the earlier, the recent and the surrounding areas revealed eight 'clocker droppings' (sensu Bendell and Elliot 1966).

This female was located the next day along the edge of a stand of shrub that bordered on the grassland area and was within 25 m of the above sites. She may have been going on or returning from a feeding trip on this latter occasion.

Post-nestingBrood-rearing FemalesMovements and Home Range

Eleven females were tracked during the post-nesting period. Table 20 shows the mean home range sizes and dimensions for these birds. Females with broods less than two weeks of age had significantly smaller home ranges compared to females with older broods. Length-to-width ratio suggests they were circular at this time. Their home ranges did not usually include the nest site. Only once was the nest site within the brood range (female 1-8.4). This female's home range was the smallest, at 3.8 ha.

How long females remained at the nest site after hatching was not accurately determined. One female (4107) I flushed from a nest at 08:13 hr on 13 June 1977 was brooding her young there. The weather was cool (13.5 C) with light intermittent rain. She returned to the nest by 13:35 hr and was presumably brooding her young again there. Air temperature was 12 C and it was raining. At 19:35 hr (temperature 19 C) the female was 45 m from the nest brooding her young. Rain had stopped at 18:20 hr. Another female (6486B) brooded her newly hatched young about 5 m from the nest. Weather conditions were also cool and rainy at this time.

Table 20. Home range characteristics of post-nesting females.

Females	Mean Home Range Size (ha)	Length/Width Ratio
With broods < 2 weeks age ¹	8.3 ± 1.26	1.37
With broods > 2 weeks age ^{1,2}	30.0 ± 3.88	2.19
Broodless ²	20.7 ± 3.08	3.15

¹Mann Whitney $U_{5,6} = 0$, $P < 0.05$

²Mann Whitney $U_{5,6} = 3$, $P < 0.05$

Mean daily distances moved during the early brood period ranged from 44 to 234 m (Fig. 11). Females usually moved in one direction away from the nest site for the first few days after hatching (Fig. 12). Broods were more mobile the second week as compared to the first. Female 1-8.4, having the small home range made short daily movements, usually less than 100 m, between a forested area and a grassy clearing. Other females did not follow such a rigid pattern and were only occasionally located at the same site twice. From dusk to dawn monitoring, I found that most movement took place during mid-morning and late afternoon. During early morning, mid-day and near dusk females with broods were fairly sedentary (Fig. 13). During early morning and late evening females were most often brooding young, as illustrated by female 6486B that was flushed at 07:25 hr on a cool (14 C) morning with heavy dew. From tracking it appears that brooding may occur at any time, depending on weather conditions.

Summer home ranges of females with broods older than two weeks were larger than the early brood range and more elongate in shape (Table 20). They were usually centered around one or more grassy, open areas.

Minimum daily distances moved by broods two to 10 weeks of age were not significantly different ($F_{6,31} = 1.78, P > 0.05$), when brood age was compared.

Figure 11. Mean daily distance (m) moved by females and broods in relation to brood age. Horizontal line is the mean and vertical bar is 95% C.I. Sample size is above vertical bar.

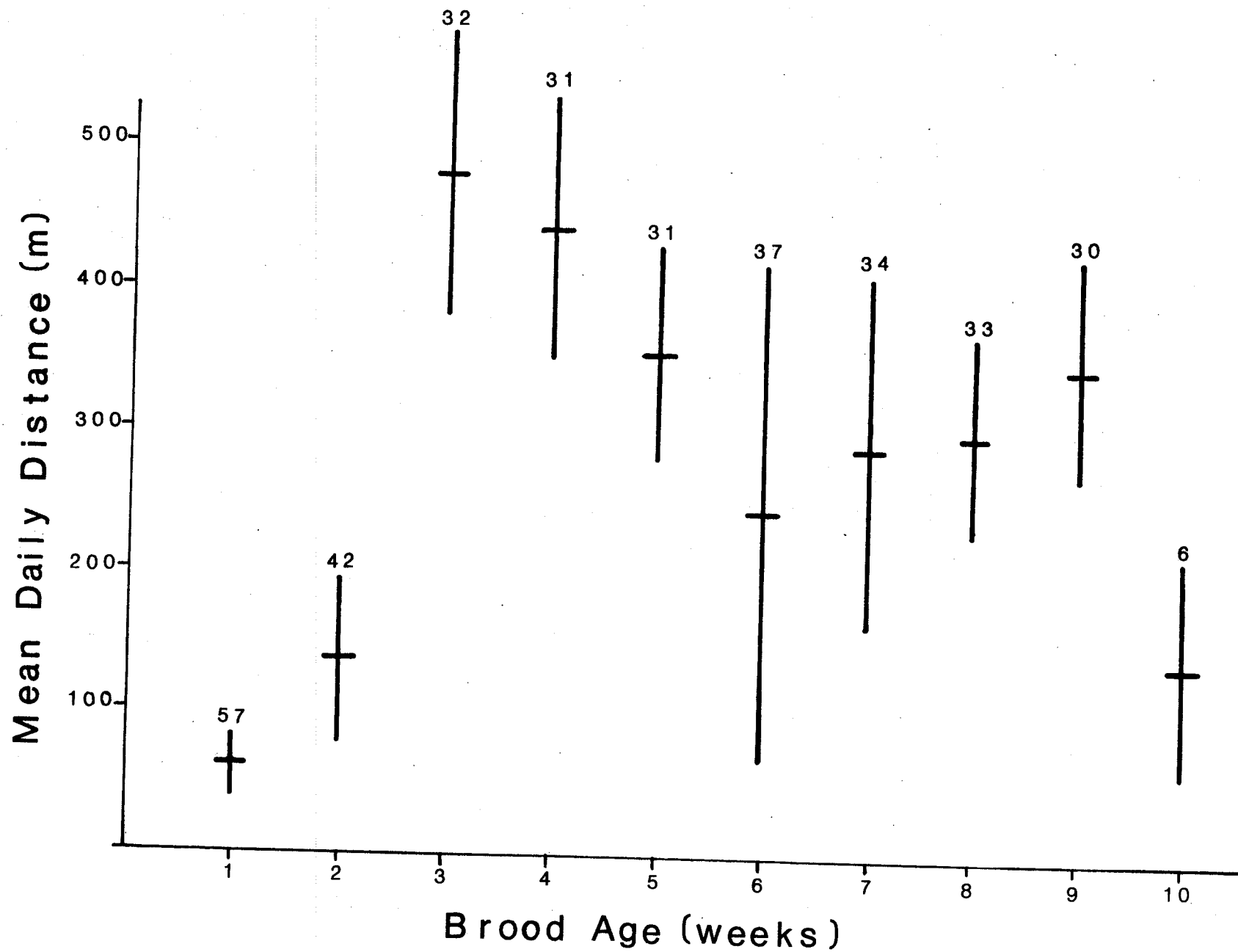


Figure 12. Movements of female 4107 and brood for days 1-3 post-hatching. Solid line is day 1, dotted line day 2 and broken line day 3. N marks nest site.

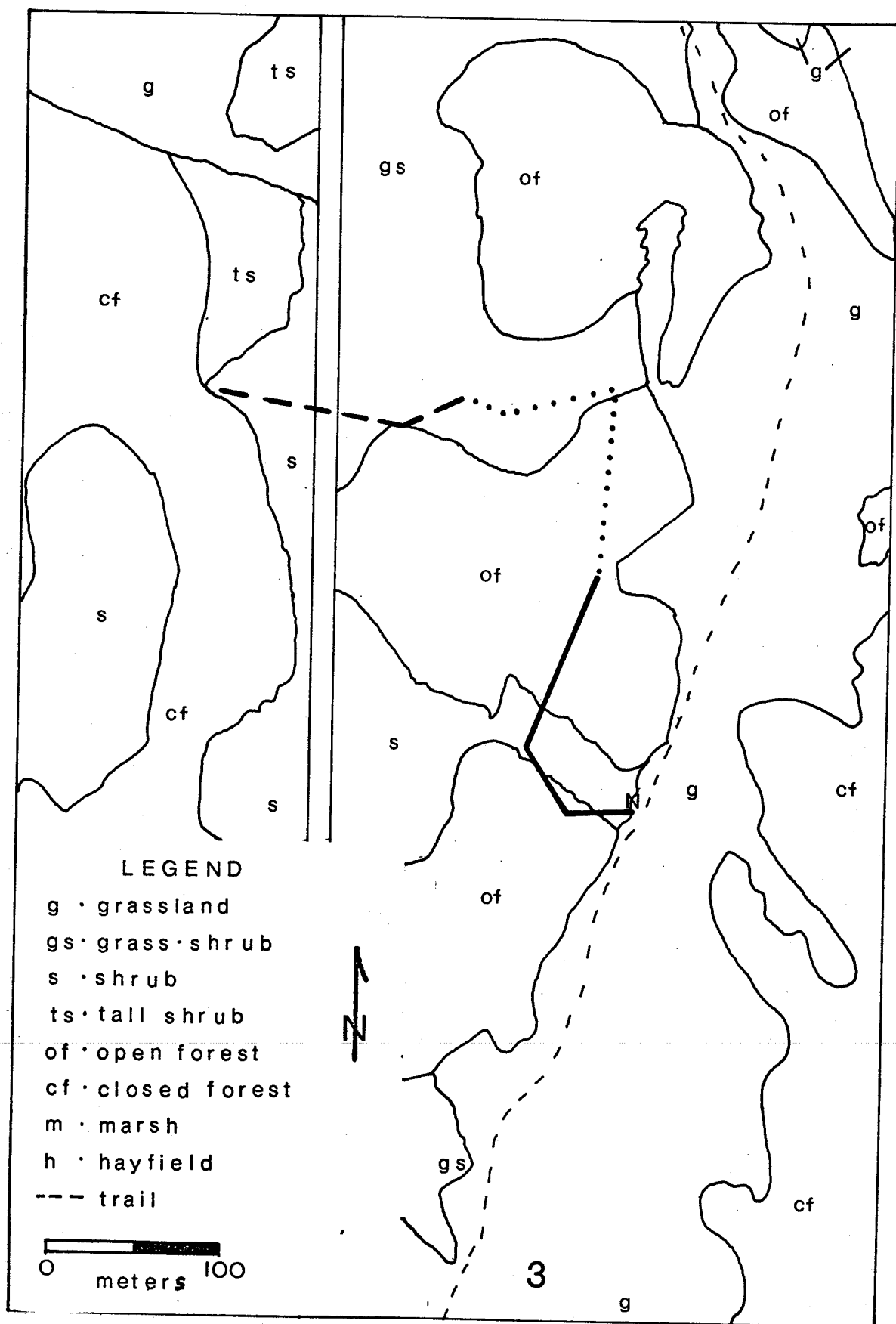
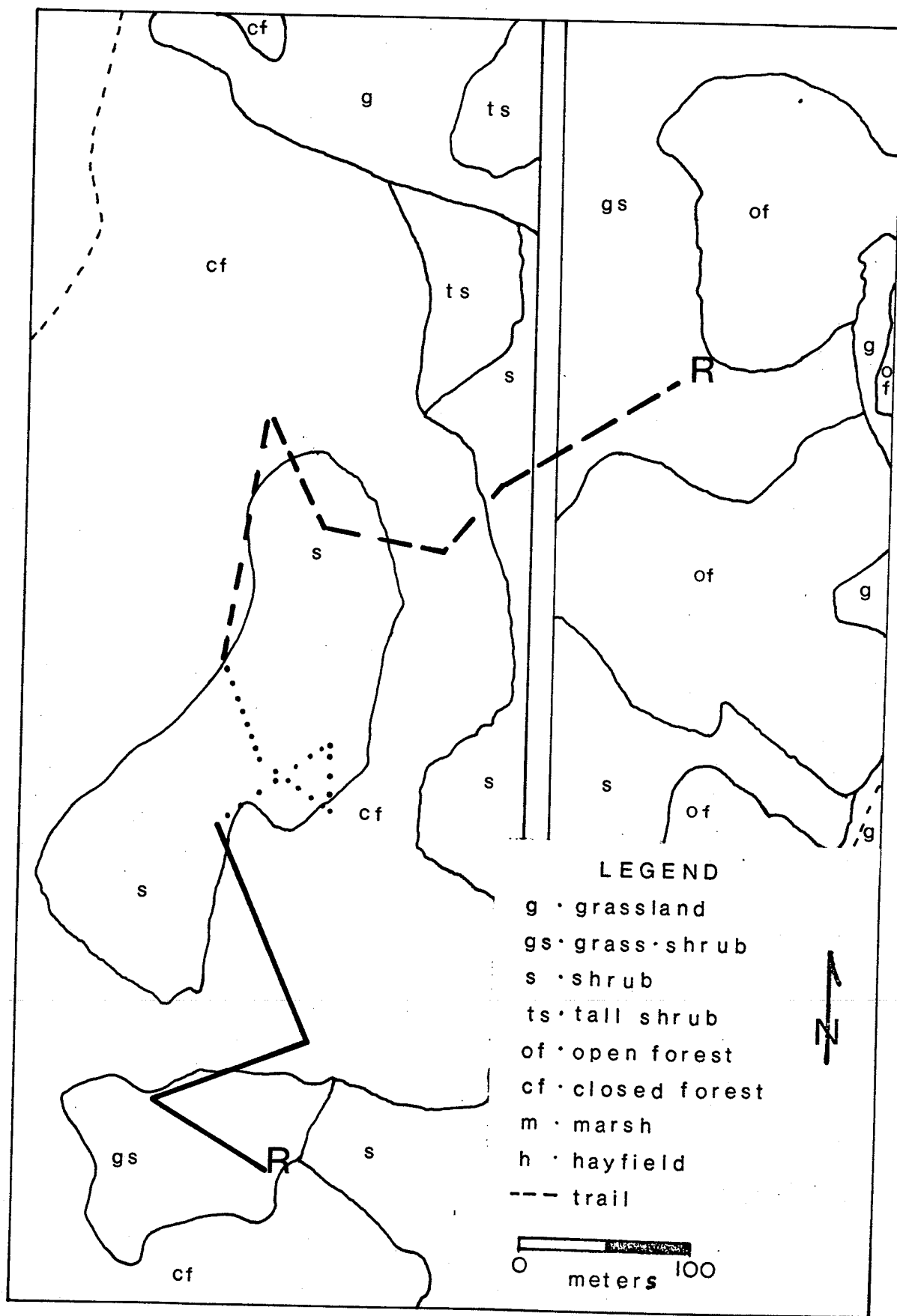


Figure 13. Movements of female 4107 and brood
(<2 weeks age) tracked hourly.
Solid line is 0800-1000, dotted line
1001-1600 and broken line 1601-2100.
Night roosts are marked by R.



Maximum distance moved by a brood in one day was 1.4 km. Most movement was done by walking. One female (4104) moved over 2 km during two days, all within her summer range.

From dawn to dusk monitoring I found the daily movement patterns for broods two to 10 weeks of age similar to young broods (Fig. 14). Morning and evening feeding areas were not always the same sites whereas the same night roost was often reused. Day and night roosts were never the same site.

Summer home ranges only once included part of the early brood ranges (Fig. 15). Female 4107 used the area near her nest when her brood was about six weeks old. She was never located at or within 50 m of her old nest site. Other females used areas adjacent to their early brood range, but were never near their nest sites.

Home Range Overlap

Unmarked females with broods were sometimes seen in the home ranges of marked females. Over a four day period four observations of an unmarked female were made, presumably the same bird (Fig. 16). The first three were within the home range of female 4107. At one point the broods were less than 100 m apart. The fourth sighting was made two days after the first observations and was outside 4107's summer range. I suggest the same

Figure 14. Movements of female 4107 and brood
(>2 weeks age) tracked hourly.
Solid line is 0700-1000, dotted line
1001-1600, broken line 1601-2100.
Night roosts are marked by R.

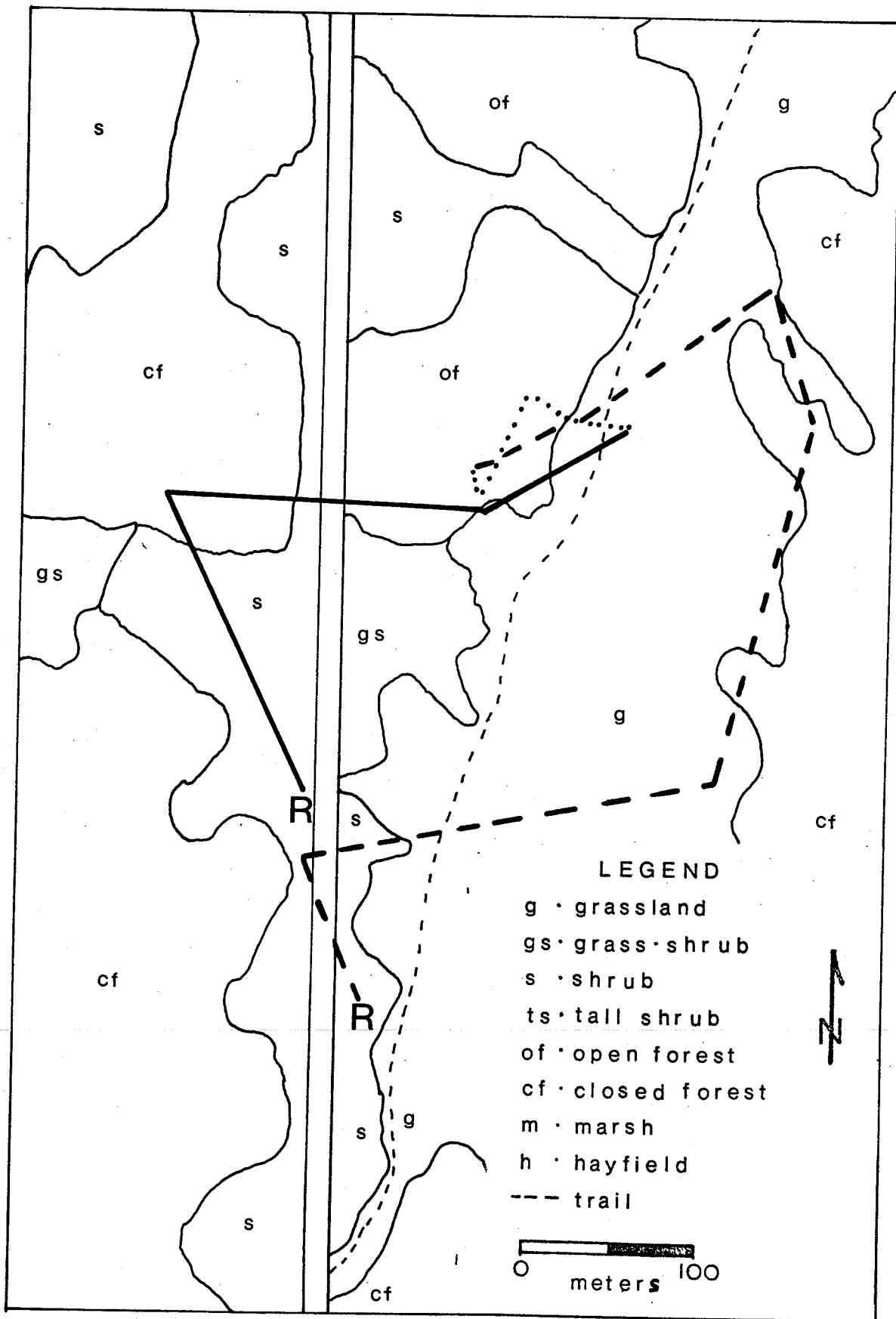


Figure 15. Post-nesting home ranges of female 4107. Broken line encompasses range for brood age <2 weeks and solid line range > 2 weeks. Nest location is marked by "N".

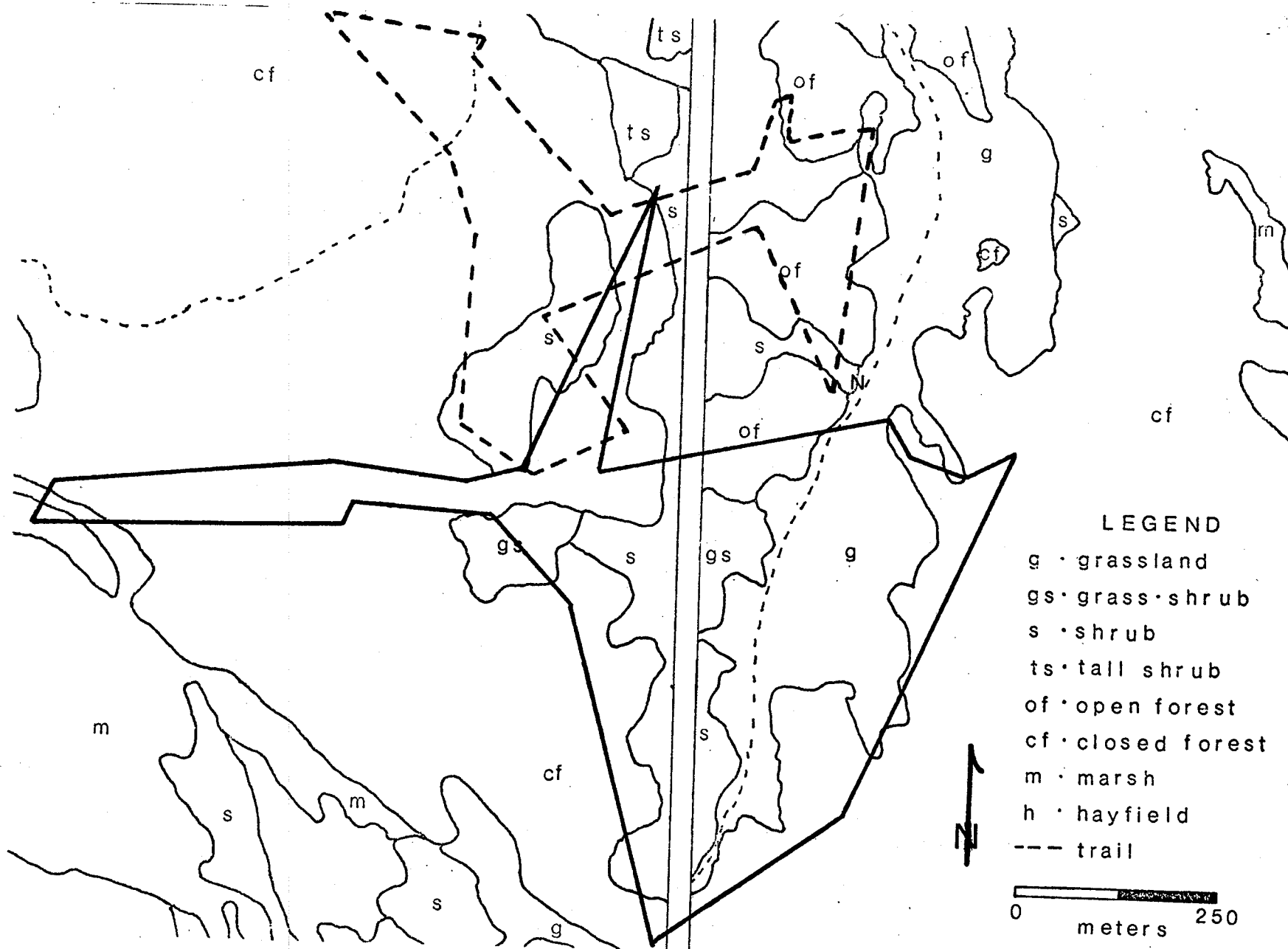


Figure 16. Home range of female 4107 and unmarked female with brood. Locations of unmarked female referred to in text are designated by "B".



female and brood were involved in all cases as the area was less than one ha in size and the same number of young were flushed each time. Further, no other females or broods were located in that area before or after these observations were made.

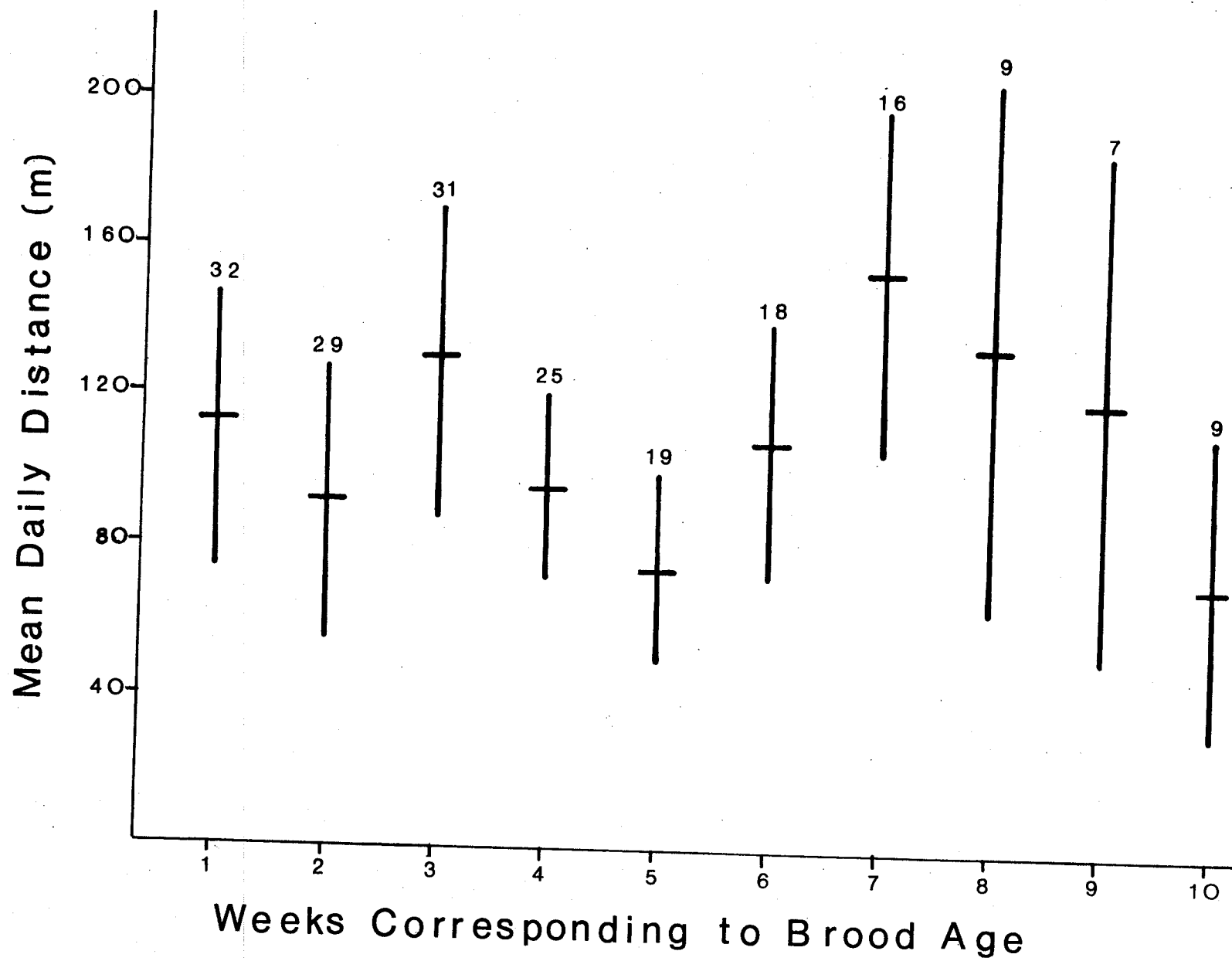
Unmarked broods were flushed four times in the summer range of female 4101 but were never closer than 200 m to this female. These broods may have been passing through the area (see section on late summer shift) as the observations were made in mid-July 1976.

Broodless Females

Movements and Home Range

Five instrumented broodless females were monitored during the post-nesting period. There was a significant difference (Table 20) in home range size between broodless and brooding (summer range) females. Broodless females were more sedentary than brooding females, especially in mid-summer. Figure 17 shows the average daily movements over the "brood rearing season" for broodless birds. That is, the corresponding period for weeks represents the age the broods would have been if the broodless females had been successful. There was no significant difference ($F_{8,27} = 1.78, P > 0.05$) in the distance moved when weeks were compared. There was a significant difference ($t = 3.02, 8 \text{ d.f.}, P < 0.05$) when brooding and broodless females were compared on a weekly basis.

Figure 17. Mean daily distance moved by broodless females during post-nesting. Horizontal line is the mean and vertical bar is 95% C.I. Sample size is indicated above vertical bar.



In week 10 a broodless female (6493) exhibited some unusual movements (Fig. 18). She moved only short distances daily (mean 107.2 m) on her summer range. Between 9 August and 11 August 1976 she moved 2.7 km. She stayed in the new area moving only about 100 m each day until I left the study area on 15 August. On 9 October her signal was relocated and I found her remains 200 m from her last known location for August. She had been killed by an avian predator during that period.

Home Range Overlap

Overlap in home ranges occurred between brooding and broodless females. The summer brood range of female 6490 overlapped with the range of broodless female 6487 between 13 July and 26 July 1976 (Fig. 19). Most locations were along the northern periphery of 6490's summer range and the females were never closer than 200 m. Although the overlap seems extensive, 6487 usually confined her activity to the northern part of her summer range.

Unmarked females with broods were flushed three times in the home range of broodless female 4102. All sightings were made after mid-July 1976 and may have been birds undergoing a shift in home range (see below).

Figure 18. Shift in home range of broodless female 6493. Arrows represent movements after shift. The "+" is the location where the female was found dead.

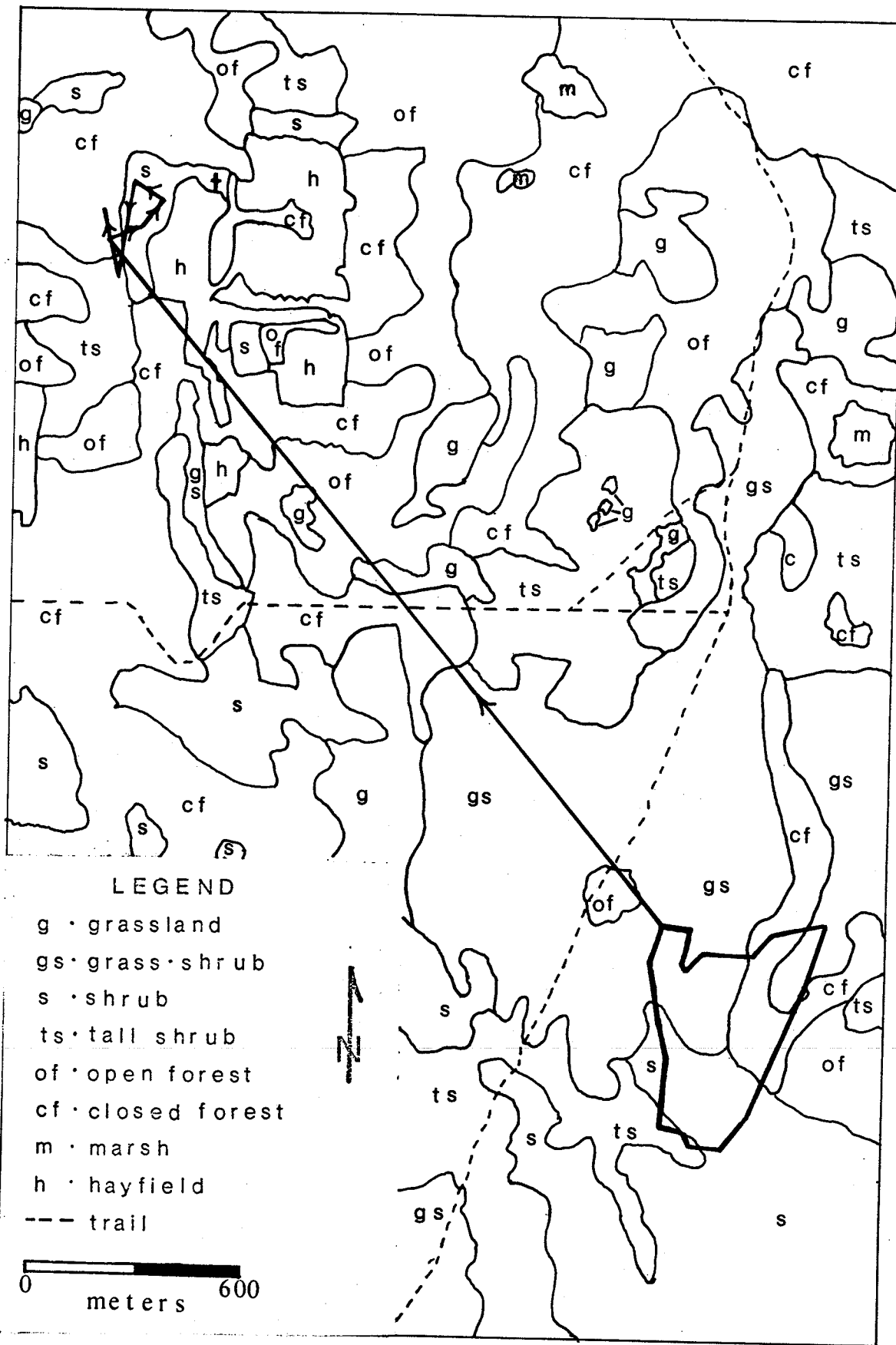
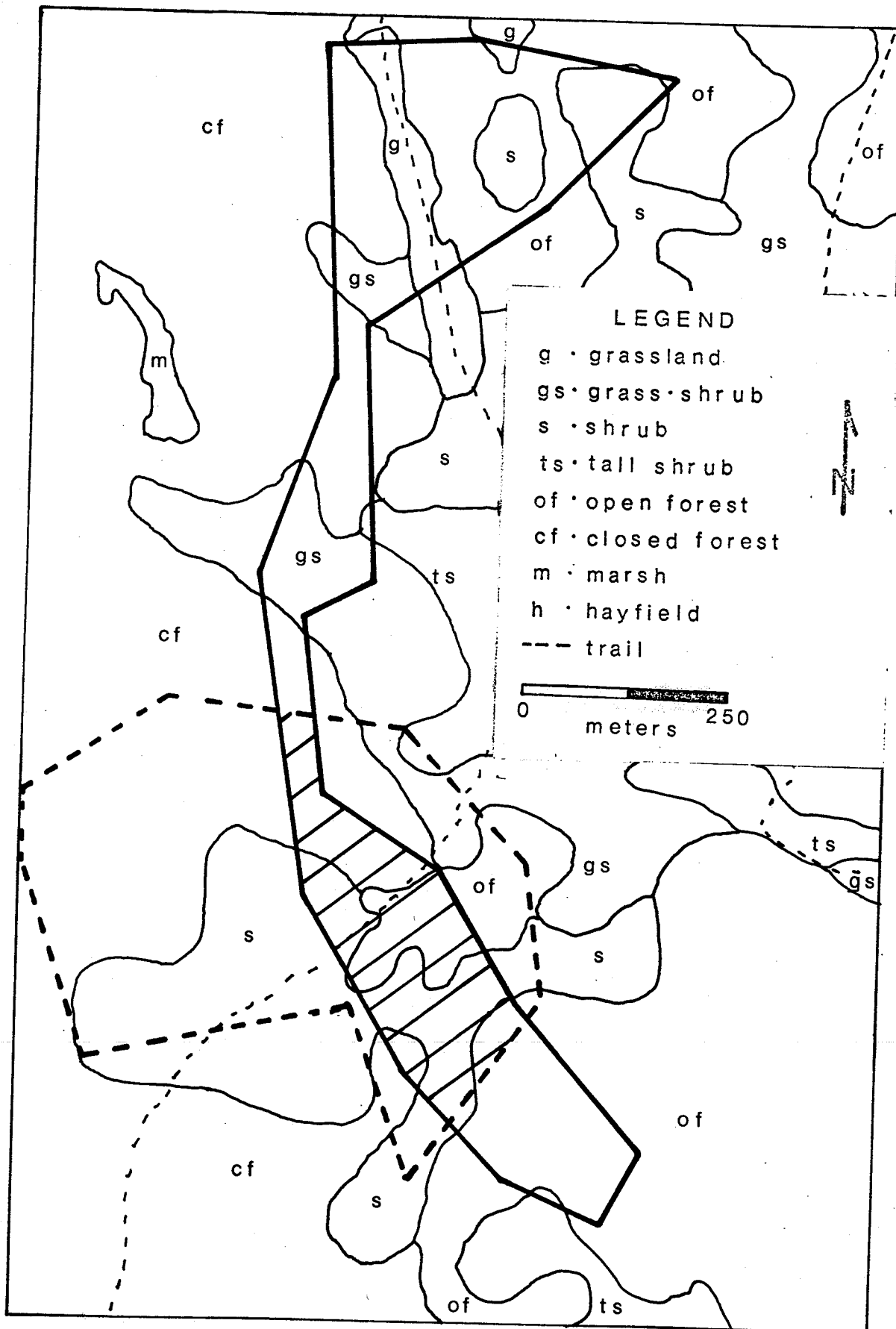


Figure 19. Home range of brood-rearing female 6490 (broken line) and broodless female 6487 (solid line). Hatched portion is area of overlap.



Late Summer Shift in Home Range

Between 23 July and 5 August 1976 all females with broods I tracked rapidly shifted their home ranges (example Fig. 20). Movements by those females were direct and relatively uni-directional away from the summer range. Mean home range size in late summer was 20.07 ± 2.56 ha. None returned to her former home range following the shift. No shift occurred in broodless females in 1976 nor in brooding or broodless females in 1977.

As a result of the shift, home range overlap occurred. Females 6490 and 06B occupied adjacent summer ranges prior to the shift. These females shifted to late summer ranges five days apart. Female 6490 occupied the new range prior to 06B's arrival. The overlap period was between 6 August and 8 August; 06B's first two days in the lowland area, but the birds were never closer than 150 m (Fig. 21). On 9 August female 06B was in the northern part of her late summer range and was never located in the overlap area again, whereas female 6490 continued to use the area of overlap.

Overlap also occurred in home ranges of brooding and broodless females due to the shift. Female 4101's summer range included part of broodless female 6487's summer range but they were never located closer than 100 m. The shift by female 4101 occurred on 4 August. She was located in the overlap area on 5 and 6 August but not after these days.

Figure 20. Shift in home range of brood-rearing female 6490. Solid lines encompass home range before shift and broken lines enclose the home range after the shift. Arrows denote movements during shift.

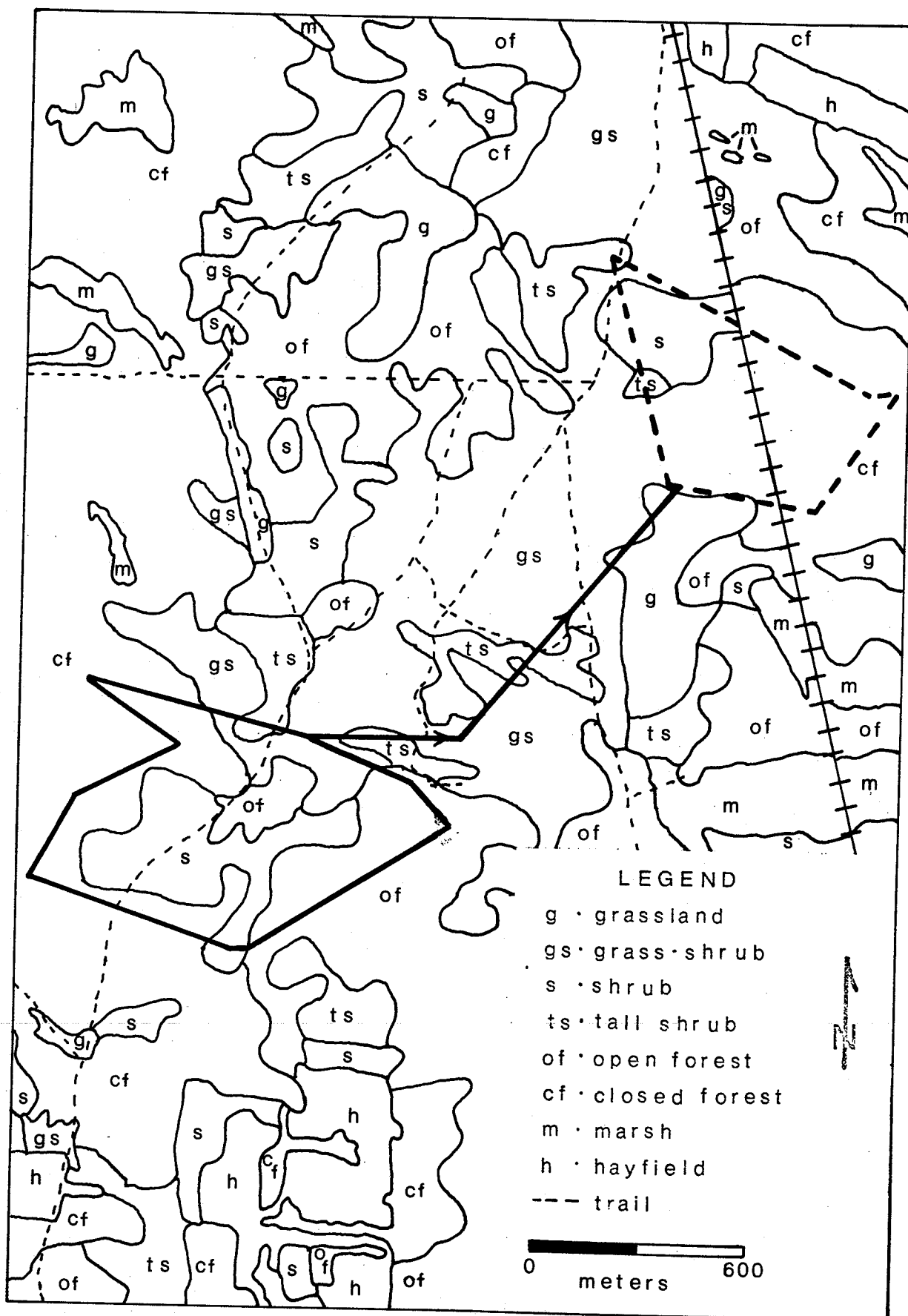
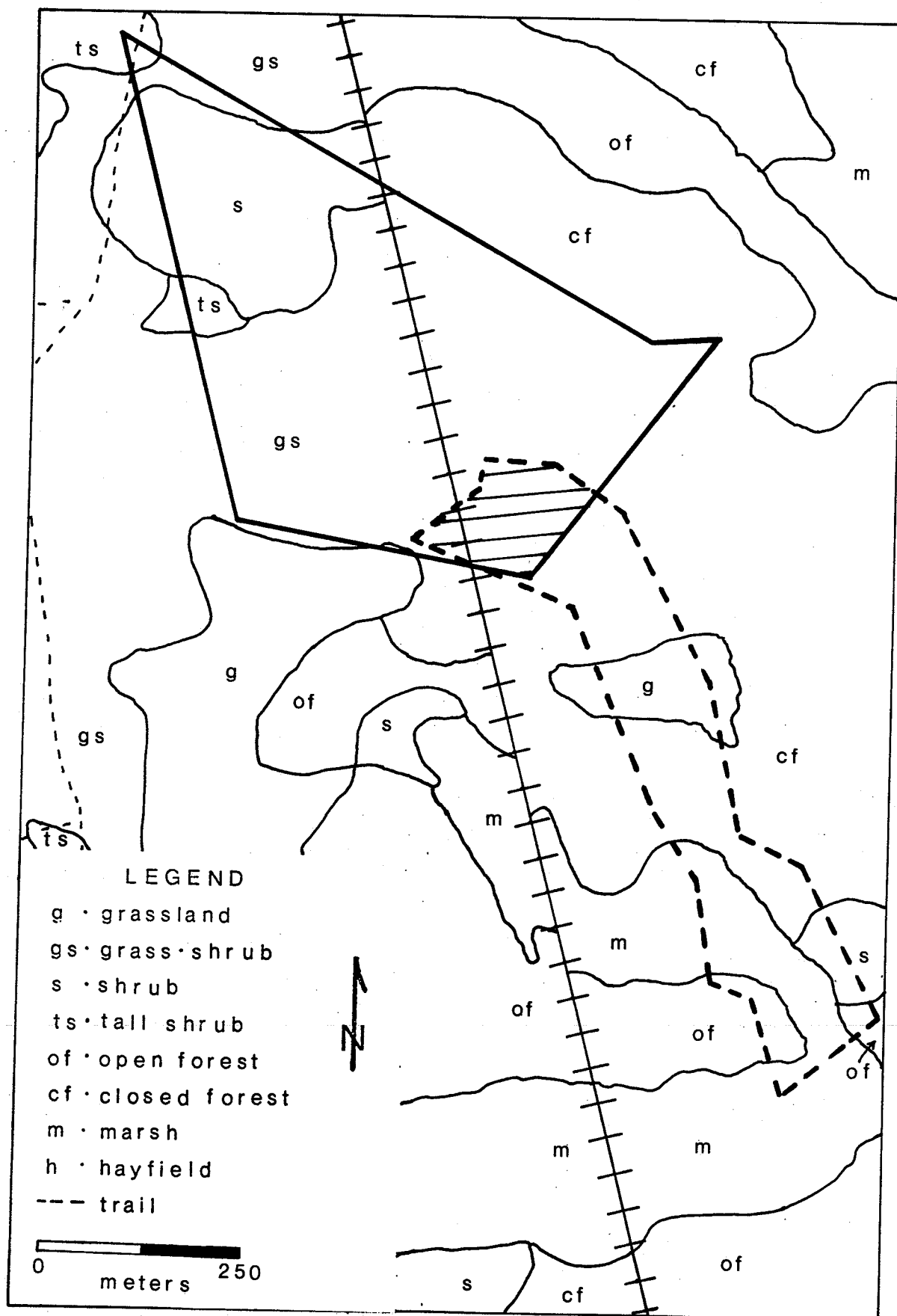


Figure 21. Home ranges (after shift) of brood-rearing females 6490 (solid line) and 06B (broken line). Area of overlap is hatched.



Habitat Use

Brood-rearing and Broodless Females

Habitats used by females rearing broods were similar during both study years ($\chi^2 = 7.40$, 5 d.f., $P > 0.05$). Females made similar use of habitat types over the course of brood rearing (Fig. 22) and there was no significant difference ($\chi^2 = 4.32$, 4 d.f., $P > 0.05$) in use when females with broods less than two weeks of age were compared to older broods. During the brood rearing period open habitat types (grass or grass-shrub) were used over 50% of the time and tall shrub was rarely used.

Habitats used by broodless females were plotted over the biweekly periods corresponding to projected "brood age" (Fig. 23). There was no significant difference ($\chi^2 = 4.02$, 3 d.f., $P > 0.05$) in habitat types used between the two study years. Broodless females used forest and shrub habitat extensively but seldom used grasslands. Habitat use was similar over the summer and no significant difference ($\chi^2 = 3.88$, 3 d.f., $P > 0.05$) was found when early (less than two weeks) and later summer periods were compared.

Brooding females differed in habitat types used ($\chi^2 = 55.2$, 5 d.f., $P < 0.05$) compared to broodless birds. Brooding females used grasslands, grass-shrub and shrub more often and tall shrub, forest and marsh less than their relative availability (Table 21). Broodless females used shrub habitat greater than its availability and tall shrub and marsh less so (Table 22).

Figure 22. Habitat types used by females with broods during post-nesting.
(n = 333 locations)

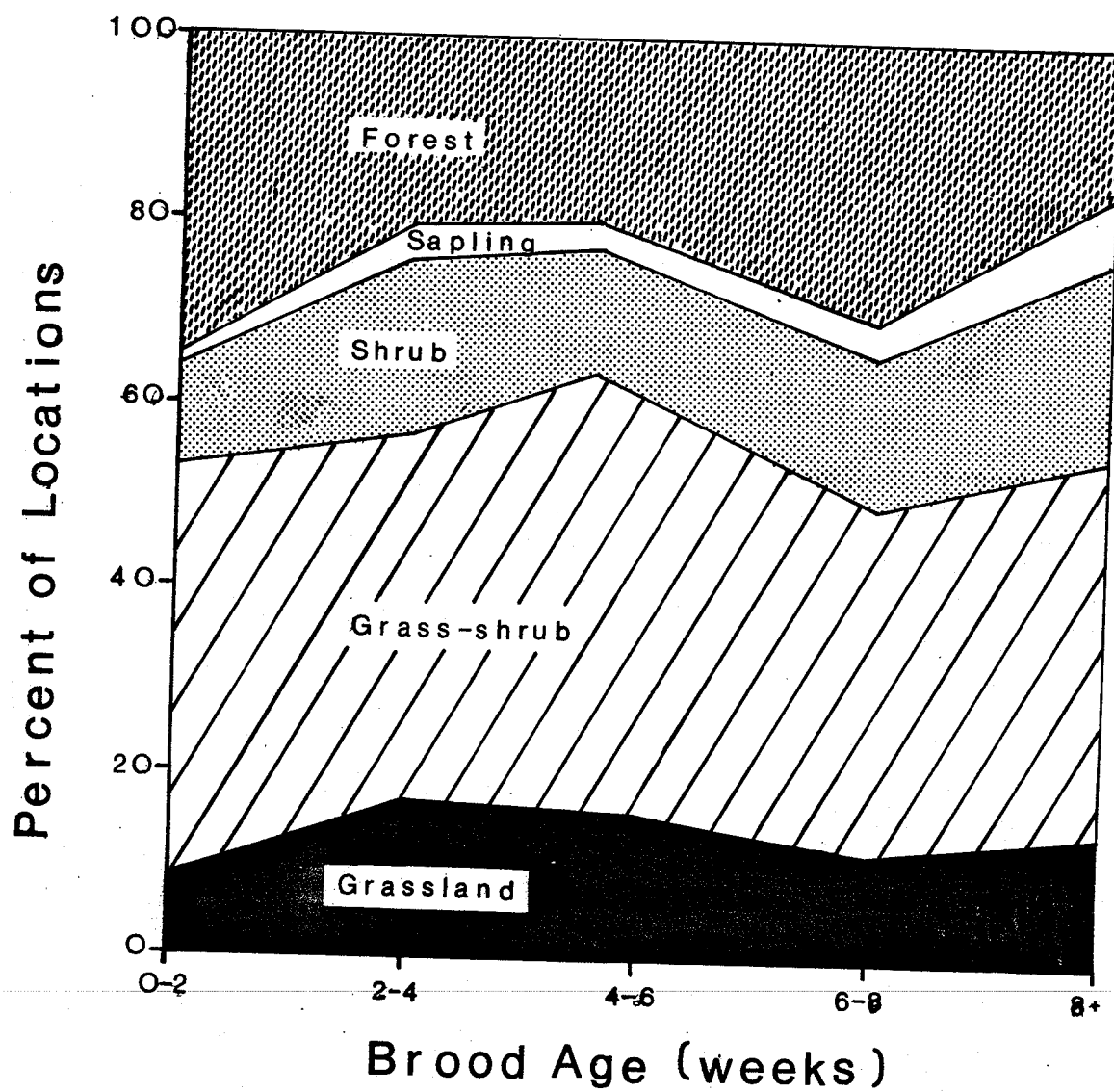


Figure 23. Habitat types used by broodless
females during post-nesting.
(n = 170 locations)

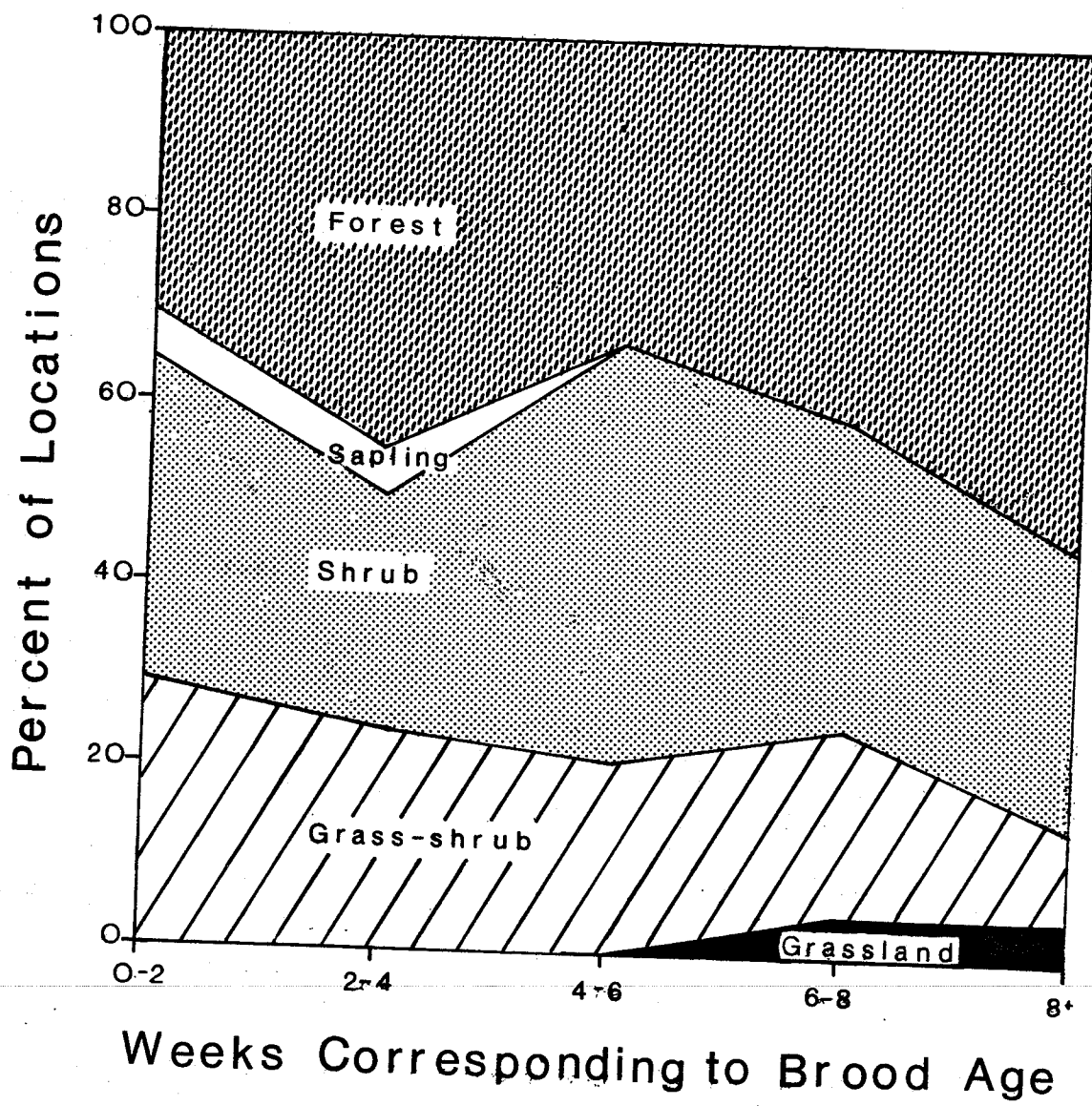


Table 21. Habitat types used by brood-rearing females in relation to habitat availability.

Habitat Type	Used ¹ (%)	Available (%)	χ^2	Significance Level
Hayland	1.2	2.7	1.93	n.s.
Grassland	9.3	4.9	13.18	.001
Grass-shrub	44.7	12.0	297.67	.001
Shrub	17.7	8.0	39.04	.001
Tall Shrub	2.7	12.0	23.98	.001
Open Forest	21.6	42.2	34.00	.001
Closed Forest	2.7	13.5	28.93	.001
Marsh	0.0	4.7	15.69	.001

¹n = 333 locations

Table 22. Habitat types used by broodless females
in relation to habitat availability.

Habitat Type	Used ¹ (%)	Available (%)	χ^2	Significance Level
Hayland	0.0	2.7	-	-
Grassland	1.8	4.9	3.42	n.s.
Grass-shrub	12.4	12.0	0.02	n.s.
Shrub	38.2	8.0	193.61	.001
Tall Shrub	5.3	12.0	6.37	.02
Open forest	34.7	42.2	2.40	n.s.
Closed forest	7.1	13.5	5.29	.05
Marsh	0.6	4.7	5.23	.05

¹n = 170 locations

Brood-rearing females used open areas more and were sometimes found long distances from dense cover. They regularly crossed large open areas whereas broodless females remained along the periphery and travelled along their edges in dense cover. For locations of females in open areas, brood-rearing females were located more often ($t = 5.31$, 49 d.f., $P < 0.05$) farther from forest or shrub cover than broodless females.

Females with broods used open habitats 50% of the time before 08:00 hr and over 70% of the time after 18:00 hr, with the greatest use of grasslands occurring in the evening (Fig. 24). Mid-day was usually spent in denser cover; generally with a canopy. Broodless females used open areas in early morning and from late afternoon but returned to denser cover earlier in the morning than did brooding birds (Fig. 25). Use of forest and shrub cover at dawn and dusk suggests that night roosting occurred there. Use of shrub habitat by brooding females for night roosts was confirmed by flushing females at sunrise and sunset from such sites as well as locating females at the same site one evening and the following morning. Cover board readings for "average" (*sensu* Pepper 1972) days (warm, dry days) (Fig. 26) were significantly different ($F_{7,198} = 4.62$, $P < 0.05$) over the course of the day. The high readings near sunrise (<06:00 hr) and dusk (>21:00 hr) correspond to the dense cover used for night roosts (see habitat-time plot, Fig. 22). Open areas used in the early morning and

Figure 24. Within "day" habitat types used by
brood-rearing females during
post-nesting.

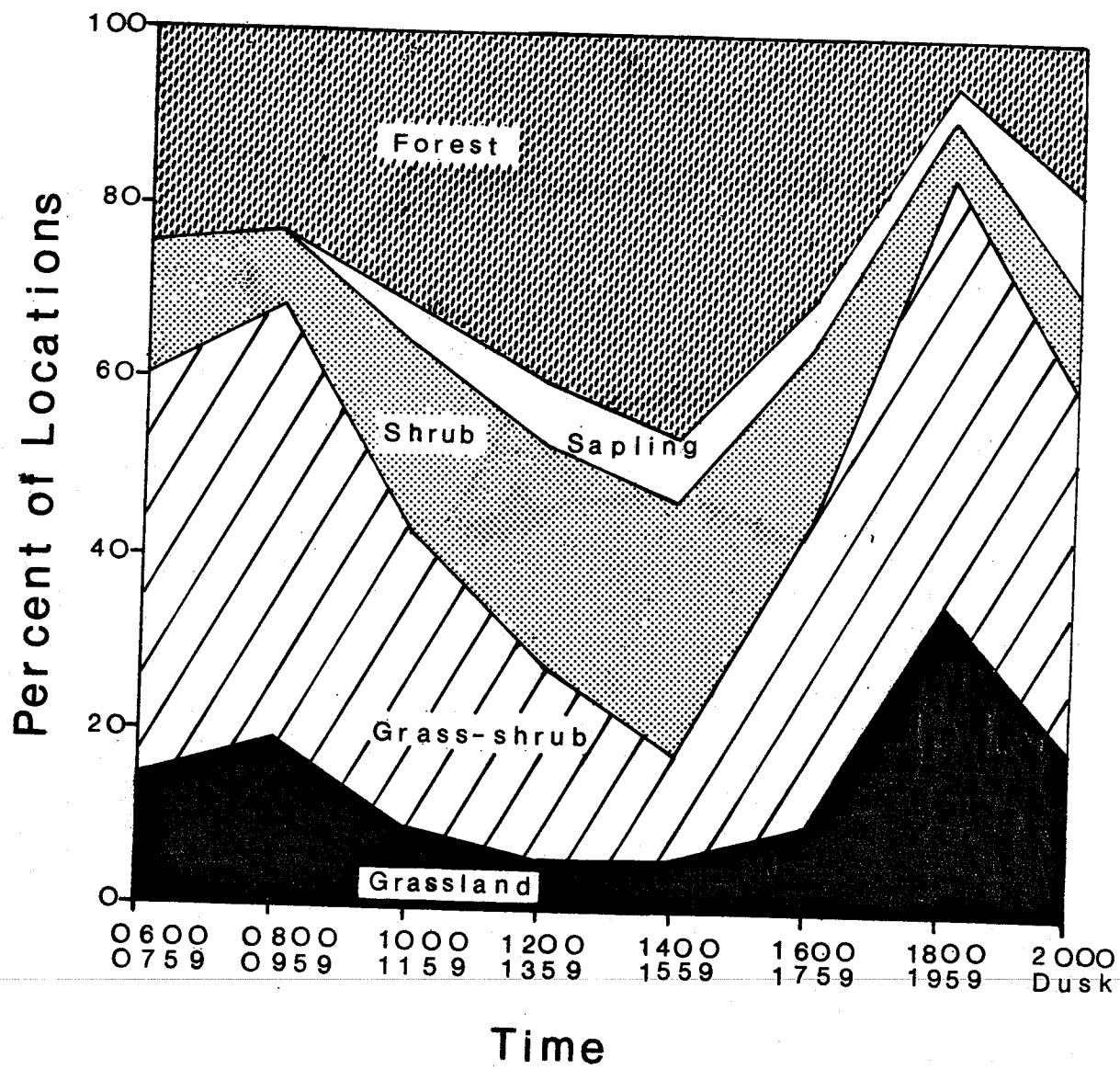


Figure 25. Within "day" habitat types used by
broodless females during post-nesting.

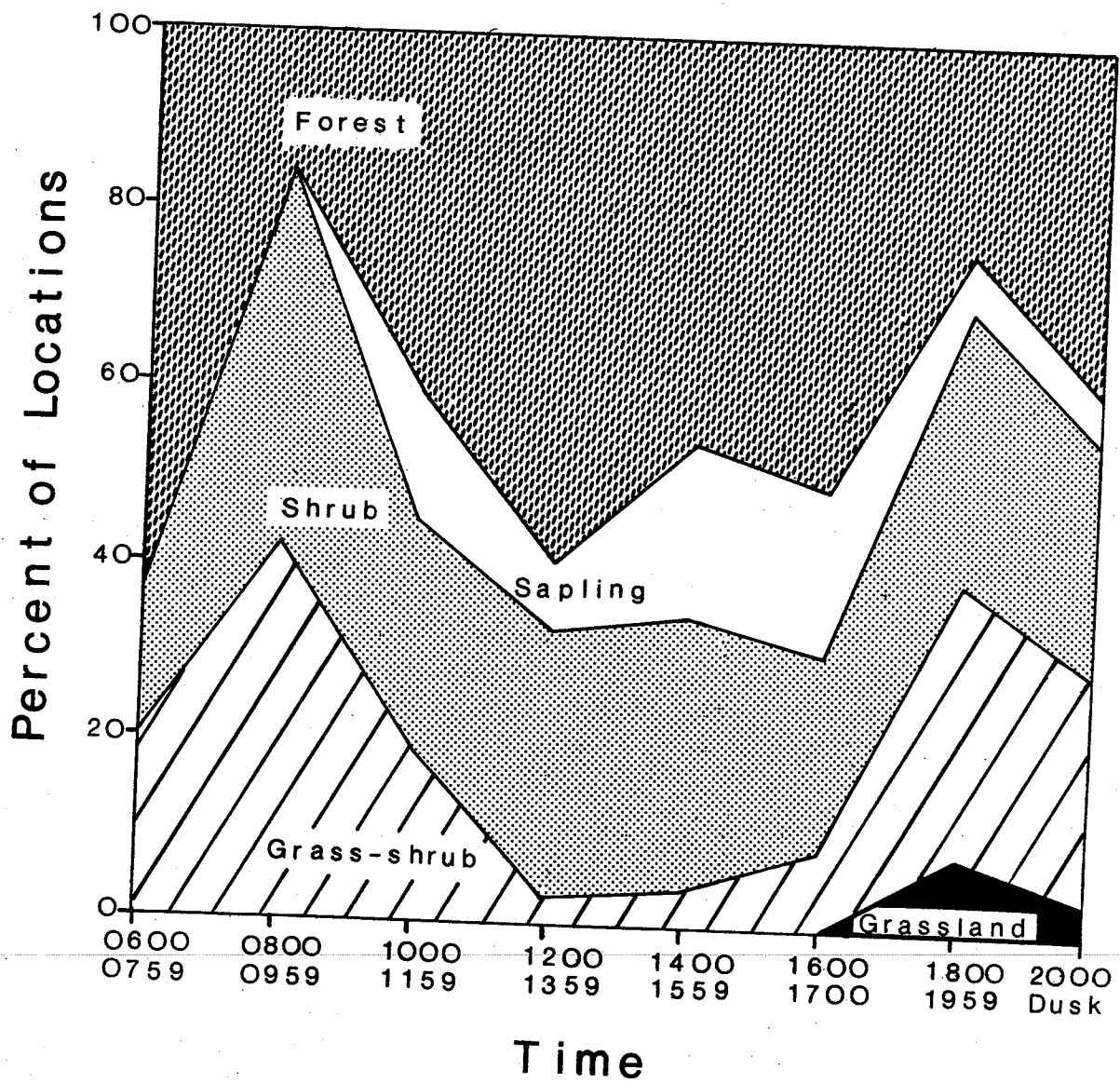
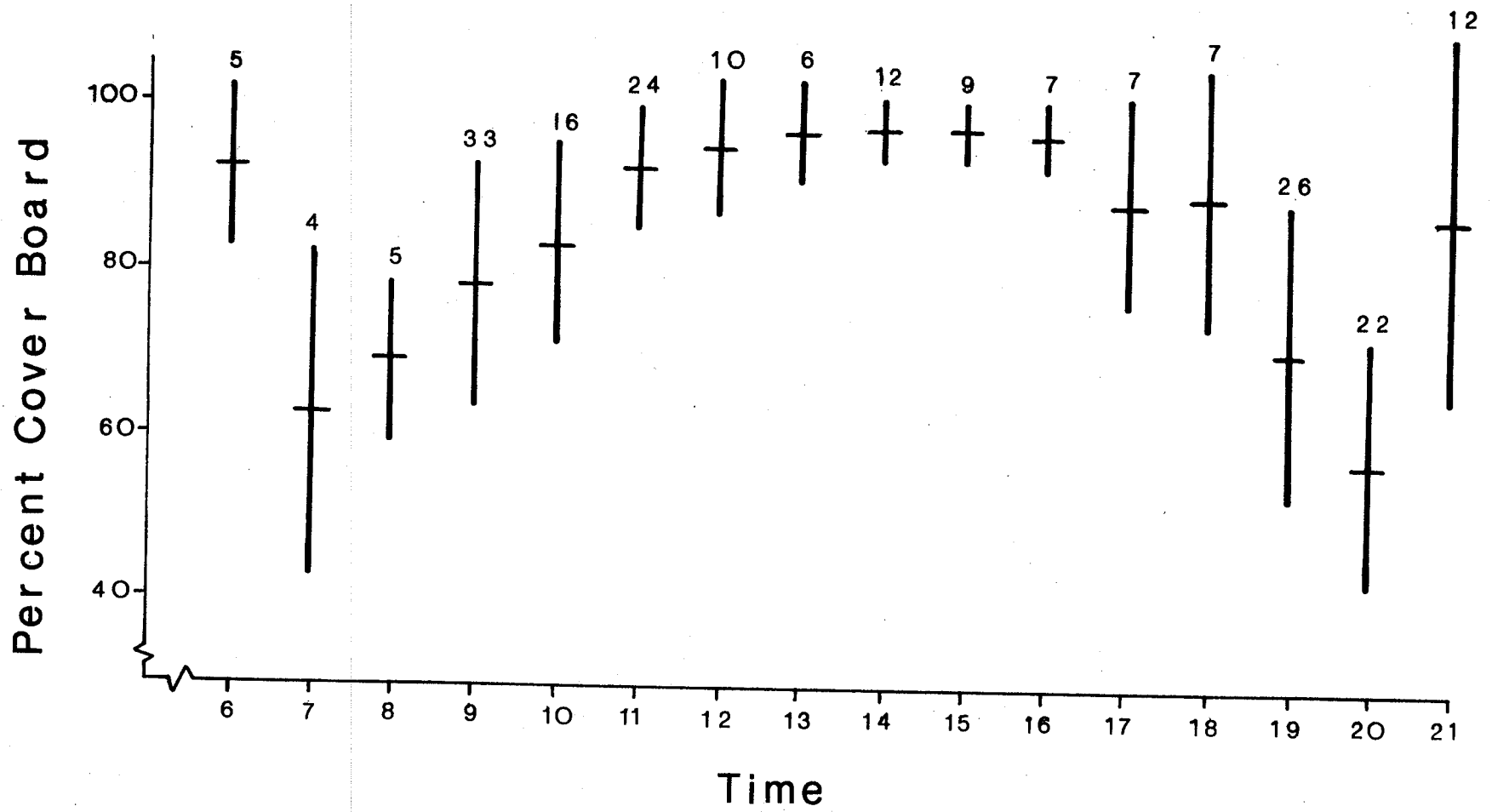


Figure 26. Cover board values at brood locations on "warm, dry days" compared with time of observation. Horizontal line is mean and vertical bar 95% C.I. Sample size is above vertical bar.



evening and dense cover used at mid-day are also apparent.

During rainy or wet days the cover-time picture is almost the opposite (Fig. 27). There is a significant difference ($F_{7,45} = 3.98$, $P < 0.05$) in cover values recorded during the day, with dense cover used until mid-day. Cover values at mid-day were similar to readings taken for morning (08:00 hr) and evening (19:00 hr) on "average" days. Values for morning and evening on wet days are comparable to night roost values and lower than mid-day roost values for average days.

Brood-rearing females appeared to select activity sites according to the ambient and site temperature (Fig. 28). When ambient temperature was less than 19 C, 64% of brood sites had temperatures warmer than ambient, and above 19 C, 70% had site temperatures cooler than ambient. Generally, warmer sites exposed to sunlight were selected in early morning, during cool weather or following rainstorms. Shaded or cooler sites were most often used at mid-day.

Shrub species were in similar proportions at sites used by brood-rearing and broodless females (Table 23), although a few exceptions are evident such as Symphoricarpos, Salix, and Betula. Densities were similar, however, for these species at brooding and broodless sites. Although upland shrubs (Populus, Amelanchier, Rosa and Symphoricarpos) predominate at sites used by all females, greater use of sites with lowland shrubs (Salix, Betula) and less of

Figure 27. Cover board values at brood locations on "rainy or wet days" compared with time of observation. Horizontal line is mean and vertical bar 95% C.I. Sample size is above vertical bar. On the time scale each figure represents a two hour interval.

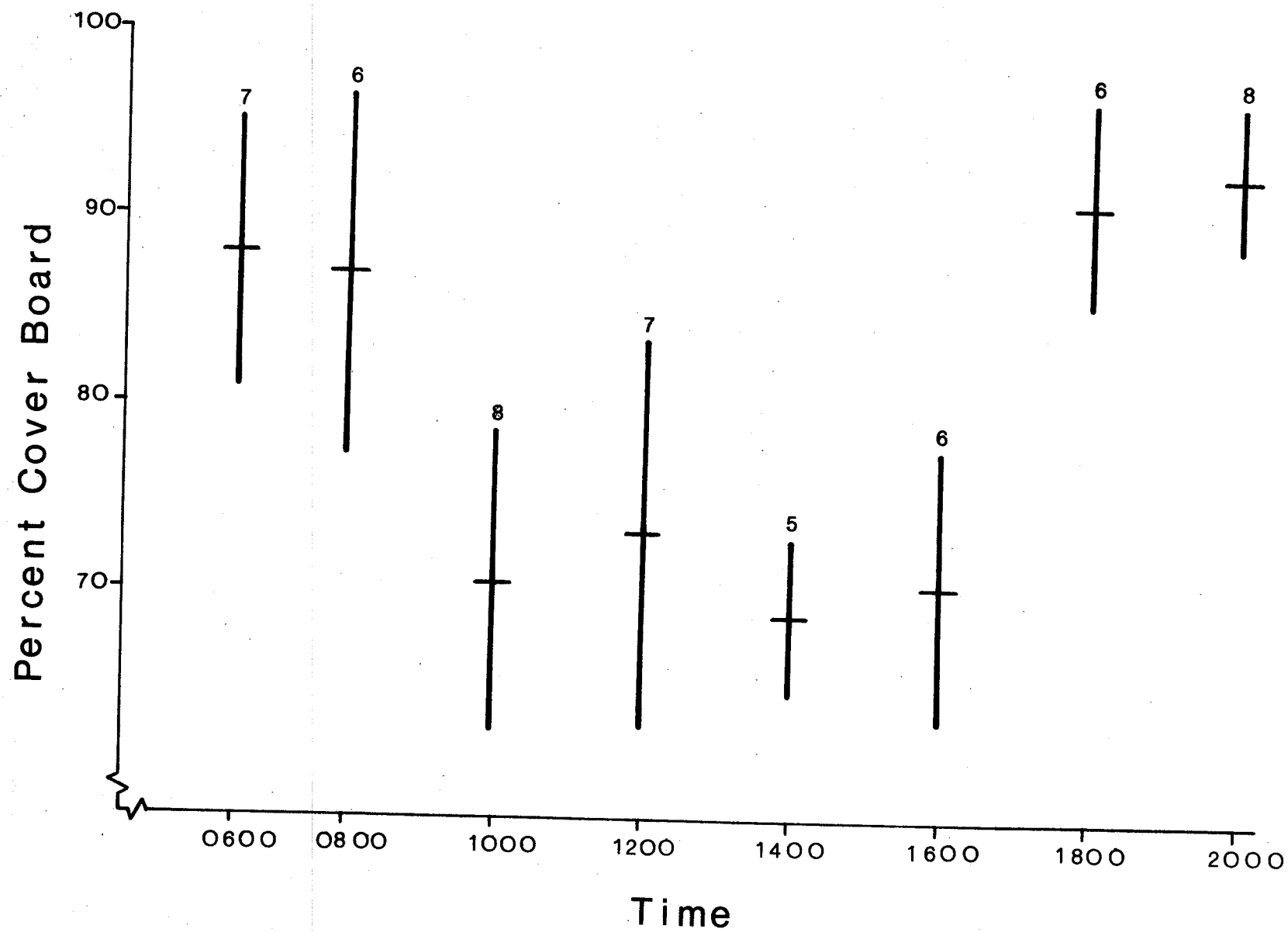


Figure 28. Variation in brood site temperature with ambient temperature. Line indicates equal ambient and site temperature. (n = 154 locations)

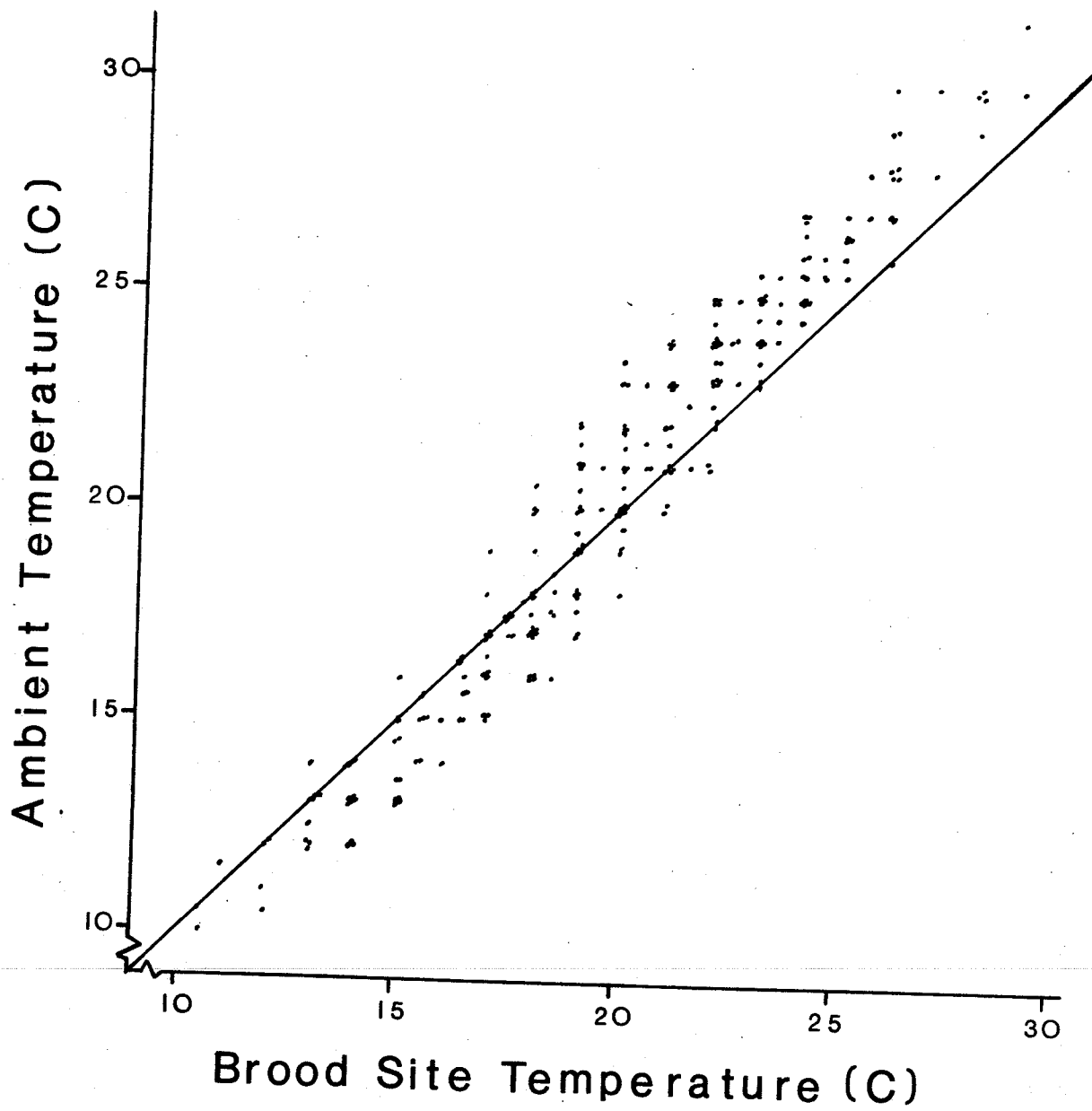


Table 23. Frequency and density of shrubs at activity sites of brood-rearing and broodless females.

Shrub Species	Brood Sites (n=217)		Broodless Sites (n=98)	
	Frequency (%)	Mean Density (/m ²) ¹	Frequency (%)	Mean Density (/m ²)
<u>Populus</u>	82.4	5.5 ± 0.5	80.6	5.1 ± 0.4
<u>Amelanchier</u>	68.3	7.0 ± 0.8	61.2	7.1 ± 0.5
<u>Rosa</u>	66.5	4.7 ± 0.6	69.2	5.6 ± 0.4
<u>Symphoricarpos</u>	11.9	18.7 ± 1.1	7.1	11.0 ± 2.4
<u>Potentilla</u>	40.8	6.7 ± 0.7	24.5	7.9 ± 1.2
<u>Arctostaphylos</u>	16.9	-	15.3	-
<u>Salix</u>	13.4	6.9 ± 0.8	27.5	9.3 ± 1.5
<u>Prunus</u>	9.7	2.2 ± 0.5	7.1	2.6 ± 0.7
<u>Betula</u>	8.1	10.1 ± 1.8	23.5	12.8 ± 1.4
<u>Shepherdia</u>	2.8	2.9 ± 1.1	2.0	1.5
<u>Lonicera</u>	1.8	1.1 0.8	1.0	4.0

¹Density of shrubs per m²/total number of sites in which it occurs.

Symphoricarpos suggest broodless females are in lowlands more often. Grass and forb frequency and cover ratings (Table 24) do not substantiate this suggestion as forbs common to lowlands were in similar frequencies at both sites.

Habitat Use During Late Summer Shift

Habitat types used by females before and after the shift were not significantly different (Table 25). Greater use was made of sites with lowland shrubs (Salix, Betula) and less of those with upland species (Arctostaphylos, Symphoricarpos, Shepherdia) but the differences were slight (Table 26). The shift was in the direction of lowlands, and edges of marshy areas were used by three of the four females tracked. Green, succulent vegetation was present here whereas the sites shifted from had little green growth present in late July, and became drier by August.

Table 24. Frequency and cover-rating of grasses and forbs at activity sites of brood-rearing and broodless females.

Species	Brood (n=217)		Broodless (n=98)	
	Frequency ¹ (%)	Mean Cover Rating ²	Frequency (%)	Mean Cover Rating
Graminae	88.6	2.93 ± 0.07	95.8	2.77 ± 0.14
Galium	68.4	1.64 ± 0.07	69.4	1.72 ± 0.09
Solidago	44.1	1.50 ± 0.08	40.2	1.52 ± 0.14
Fragaria	36.2	1.38 ± 0.10	36.1	1.23 ± 0.11
Lathyrus	33.3	1.42 ± 0.10	33.3	1.38 ± 0.11
Aster	28.2	1.16 ± 0.09	12.5	1.11 ± 0.19
Artemesia	26.0	1.06 ± 0.11	6.9	0.60 ± 0.22
Monarda	25.4	0.95 ± 0.10	19.4	0.78 ± 0.11
Comandra	21.4	0.89 ± 0.09	6.9	0.60 ± 0.22
Vicia	19.2	1.06 ± 0.10	13.9	1.00 ± 0.19
Thalictrum	12.4	0.45 ± 0.11	33.3	0.71 ± 0.12
Misc. Compositae	9.6	0.71 ± 0.11	12.5	0.89 ± 0.10
Carex	8.5	1.40 ± 0.05	9.7	1.00 ± 0.20
Taraxacum	7.9	1.07 ± 0.19	4.2	0.33 ± 0.27
Apocynum	7.3	1.21 ± 0.20	2.0	0.00
Achillea	6.8	0.42 ± 0.14	8.1	0.38 ± 0.17
Astragalus	4.5	0.05 ± 0.18	0.0	-
Sanicula	3.9	0.71 ± 0.17	22.4	0.68 ± 0.12
Antennaria	3.4	0.17 ± 0.15	1.0	0.00
Pyrola	3.4	0.33 ± 0.19	2.0	0.00
Medicago	2.8	2.00 ± 0.56	5.5	1.00 ± 0.32
Sonchus	2.8	0.40 ± 0.22	0.0	-

¹Species with frequency at brood sites; <2% not recorded.

²Mean cover = total cover rating/sites where species occur.

Table 25. Habitat types used by broods before and after the shift in summer home ranges in 1976.

Habitat Type	Prior to Shift	After Shift
Hayfield	3	0
Grassland	15	9
Grass-shrub	31	28
Shrub	11	12
Tall Shrub	3	5
Open Forest	16	16
Closed Forest	5	2
Total	83	73

$\chi^2_{\text{adjusted}} = 2.44, 3 \text{ d.f.}, P > 0.05$

Table 26. Frequency and density of shrubs at brood activity sites before and after the shift in home range in 1976.

Species	Before Shift (n=81)		After Shift (n=57)	
	Frequency (%) ¹	Mean Density (/m ²)	Frequency (%)	Mean Density (/m ²)
<u>Populus</u>	79.3	5.5 ± 0.4	87.7	4.6 ± 0.4
<u>Amelanchier</u>	68.7	6.8 ± 0.5	73.6	7.3 ± 0.8
<u>Rosa</u>	61.3	5.4 ± 0.6	70.2	4.9 ± 0.6
<u>Symphoricarpos</u>	45.6	7.9 ± 1.2	41.0	6.2 ± 0.7
<u>Arctostaphylos</u>	24.5	-	18.9	-
<u>Betula</u>	7.0	9.3 ± 1.9	14.7	10.0 ± 2.9
<u>Potentilla</u>	33.3	10.2 ± 1.5	12.9	19.1 ± 1.4
<u>Salix</u>	12.8	6.3 ± 1.0	20.3	8.4 ± 0.9
<u>Prunus</u>	10.5	2.4 ± 0.5	9.2	4.3 ± 1.5
<u>Shepherdia</u>	3.2	2.2 ± 1.2	1.7	1.9 ± 0.6
<u>Lonicera</u>	2.8	1.3 ± 1.0	1.8	1.1 ± 1.0

¹ Species with a frequency <2% not recorded.

DISCUSSION

Pre-incubation Home Range and Movements

I found that some female Sharp-tailed Grouse moved long distances from arenas and others remained near these sites. The existence of two such groups within the population is noteworthy. Early studies of female Sharp-tailed Grouse by Baumgartner (1939), Hamerstrom and Hamerstrom (1951) and Kobridger (1965) indicate they remain close to arenas prior to nesting, and nesting studies seemed to support this idea (Hamerstrom 1939, Pepper 1972). Artmann (1970), however, suggests that most females move the longest distances of the breeding season prior to nesting. This is supported by Robel et al. (1970) in their work on Greater Prairie Chicken.

In Sharp-tailed Grouse I tracked, Group II females' long daily movements may have been associated with mate seeking. Archibald (1975) suggests this occurs in female Ruffed Grouse (Bonasa umbellus). Group I females remained around the capture arena and did not move as far. Group II females were never located near or on capture arenas after they were released.

Group I females moved short distances during the pre-egg stage, probably searching for nest sites and feeding, dusting and roosting. Long distances moved by Group II females and infrequent re-use of sites suggest they are dispersing. Spring dispersal of females has been documented or postulated in several grouse species (Stirling 1968, Zwickel 1973, Herzog and Boag 1977). The long movements and visits to more than one arena by Group II birds are the basis for proposing dispersal in my study. As already indicated most authors suggest females move little from the area around one arena. Bowman and Robel (1977) suggest that dispersal of Prairie Chicken may continue through spring into early summer, and Robel *et al.* (1970) have documented inter-arena movements by females.

Dispersal of Group II females may be due to their social position and/or involvement in aggressive encounters. Robel (1970 a,b) and Robel and Ballard (1974) believe that aggressive interactions between females on arenas may prevent or delay breeding if subordinate birds remain at one arena. These encounters could also cause subordinate females to abandon arenas and seek others or be attracted to males displaying solitarily (Robel 1970 a, b, Sexton 1979). The Group II females I tracked may have been subordinate birds.

Aggression has been proposed as a spacing mechanism for females in other grouse (Macdonald 1968, 1970, Herzog and Boag 1977). Macdonald (1970) reported overt aggressive

encounters between female Spruce Grouse (Canachites canadensis). Herzog and Boag (1977) suggest auditory cues such as flight sounds or calls are the more common spacing mechanisms. Females vocalize when approaching arenas (see Lumsden 1965, Hjorth 1970) but birds I tracked away from arenas were silent. Caldwell (1976) reports females away from arenas giving aggressive calls. Therefore, auditory stimuli may act to space female Sharp-tailed Grouse. Whereas Robel (1970 a, b) and Caldwell (1976) felt it may space females around their respective arenas I suggest it acts to space females throughout the available habitat and forces them to move between arenas in search of suitable nest sites as well as for mating.

Observations of home range overlap support the spring spacing hypothesis. Where Group I females' home ranges overlapped, one bird continued to use the area of overlap whereas the other avoided this area. The dominant female may exclude the subordinate. Group II females may have been unable to establish a home range around a particular arena and therefore moved to other arenas.

Also, there may be a difference in age between groups. This may affect their aggressive level and hence dispersal.

Group II females may be less aggressive. They were seen more often with conspecifics. Sharp-tailed Grouse form winter flocks (Hamerstrom and Hamerstrom 1951) that are sex specific (Caldwell 1976). Aggressive interactions possibly promote spring dispersal of these flocks

(Caldwell 1976, Robel 1970 b). Therefore the association of Group II females with conspecifics may suggest they are remnants of winter flocks whereas Group I females may have dispersed or forced less aggressive birds to disperse from winter flocks. If winter ranges are closely associated with arenas, dominant females could establish home ranges nearby. Subordinates may be forced to disperse either to other arenas or away from arenas in search of nest sites or males with which they can mate. Home ranges of Group II females in association with two or more arenas support this idea.

Robel et al. (1970) tracked a female Greater Prairie Chicken that remained essentially solitary the entire winter. If this occurs in Sharp-tailed Grouse and such females have home ranges close to an arena year round, they would be at an advantage during aggressive encounters with dispersing birds. Group II females I captured in this study may have been dispersing when caught. They would pass through an area if a suitable home range was not available and not return to the capture arena.

Dispersal has also been suggested to affect predation (Bowman and Robel 1977) and population regulation in grouse (Robel 1970). Group II females were preyed upon more heavily; all birds except one were killed during the pre-egg stage, the period of greatest movement.

Home ranges were similar in Group I and II females during the egg stage and were smaller and daily movements

shorter than those in the pre-egg stage. Artmann (1970) reports similar results in female Sharp-tailed Grouse he tracked. Archibald (1975) found the opposite in Ruffed Grouse. He suggests the larger home ranges correspond to increased searching for food to meet nutritional demands of egg production. At Chatfield nest sites may have been selected relative to an abundant food supply. Only short movements from nests to feeding sites would be necessary during egg-laying and incubation. The proximity of nest sites to a supply of high energy food has been recorded in Spruce Grouse (McCourt et al. 1973) and Ruffed Grouse (Schladweiler 1968). Maxson (1978) showed that Ruffed Grouse movements are shortest during egg-laying.

The spring dispersal of females hypothesis is supported also by comparing home ranges of Groups I and II females. The greatly reduced home range during egg-laying in Group II females (similar in size to Group I) suggests that through dispersal they were all able to find suitable nesting habitat. My observations of egg-laying females agree with Watt's (1969) findings in Greater Prairie Chicken. The rest of the egg-laying stage is spent some distance from the nest, as is also reported for Ruffed Grouse (Maxson 1977).

Home range overlap between a renesting female on her second pre-egg range and an incubating female's egg-laying range is noteworthy. After locating the renester within 60 m of the incubating female I next located her over 200 m away. The renester was not located in the over-

lap area again. McBride et al. (1969) report aggressive encounters in feral Domestic Fowl (Gallus gallus) between incubating females and other females approaching these nest sites. This may have occurred in the above case or auditory spacing mechanisms (Herzog and Boag 1977) may have come into play. Interestingly the renesting female included in her second pre-egg range part of the incubating female's previous pre-egg range. As this latter bird was incubating no encounters would occur between the birds and the renester could travel through the area in search of potential nest sites.

Pre-incubation Habitat Use

Groups I and II females made similar use of habitat types. This suggests females are selecting habitats according to their requirements and move to areas that will satisfy these needs. Food, shelter, protection from predators and potential nest sites would be requirements common to both groups and a similar use pattern would be expected.

The differences in habitat used during the pre-egg and egg stages and the decreasing use of forest cover have been suggested by Marshall and Jensen (1937). They found that Sharp-tailed Grouse shifted from woody cover to grasslands in spring, possibly due to increased use of arenas at this time. This is probably true for males but to a lesser extent for females.

Changing diet or food availability may cause the shift away from forest areas. A crop from a female taken in early April contained mainly Populus buds. Sharp-tailed Grouse at Chatfield continued feeding on Populus buds until late April. A female taken just prior to egg-laying stage had eaten Lathyrus, Fragaria leaves, grass stems and three Populus buds. A laying female had eaten Galium, Lathyrus and Arctostaphylos berries.

Winter foods are tree buds (Schmidt 1936, Grange 1948) and forbs and green grass are spring foods (Grange op. cit., Jones 1966). Svoboda and Gullion (1972) noted that female Ruffed Grouse shifted their diet from aspen buds to frost-resistant forbs in early May due to reduced availability of buds as trees leaf out, and increasing growth of forbs. Campbell et al. (1966) report that Lathyrus contains high protein levels in spring. Sharp-tailed Grouse may select it because high energy food is required for egg production (Ricklefs 1974). Grasslands or grass-shrub areas would be free of snow earlier than the forest floor and spring forbs are probably more abundant in these areas during pre-incubation. Females would probably move to areas of food abundance. Forb species found in crops were common at activity sites.

Shrubs common at activity sites (Populus, Rosa, Amelanchier) are typically found in mesic sites along forest edges in the aspen parkland (Maini 1968). Comparison of activity and sample sites suggest birds are located

along an upland-lowland edge. Spring use of this edge may be an artifact of the shift from winter lowland areas (Marshall and Jensen 1937, Hamerstrom and Hamerstrom 1951) to upland nesting cover (Amman 1957, Pepper 1972). Changing habitat requirements and possibly more food along the upland-lowland edge may result in its extensive use. Also, the edge provides cover from predators in the form of shrubs whereas in open areas cover is sparse at this time.

Grasslands and forest were used in proportion to availability, and hayfields were never used. Artmann (1970) reported extensive use of native grasslands and little use of hayfields. Preference is also shown for mixed rather than pure stands of vegetation; the latter typifying hayfields (Hamerstrom 1939). Grasslands used in this study contained a mixture of native grass species and forbs. Closed forest and sapling areas were used less than their availability and may even have been avoided. Godfrey (1975) suggests that very dense stands of shrub which prevent Ruffed Grouse from walking easily are avoided.

Open areas used in morning and evening probably correspond to periods of intensive feeding. Heavier cover, used during mid-day and near dusk, acts as day resting areas and night roosts (Marshall and Jensen 1937). Prairie Chicken night roosts are usually in small patches of closed cover surrounded by large open grassy areas

(Jones 1968). Use of such areas by grouse is probably related to the screening effect, preventing detection by predators or ~~serving~~ as escape cover when necessary.

Cover board results clearly show the difference in cover provided by the different habitat types used during the day. Open cover is associated with feeding areas and is used in morning and evening. Mid-day roosts are always in dense cover. Sites with shrubs or dense residual cover are probably used due to a lack of current plant growth. Possibly as current growth becomes available grass and grass-shrub sites would be used more often for activity other than feeding. I detected no such shift, but Robel et al. (1970) found it occurred in Greater Prairie Chicken.

Daily activity patterns were consistent with Maxson's (1977) findings for female Ruffed Grouse in spring. Greatest activity was in morning and evening corresponding to feeding periods with only minimal movement during mid-day. Movement was not recorded at night roosts, as birds moved there near dusk and were still there the following morning. Christenson (1971) and Marshall and Jensen (1937) found a similar pattern in Sharp-tailed Grouse.

Use of Burned Areas

I found no nests in the burned area whereas Kirsch and Kruse (1972) found Sharp-tailed Grouse in burned grasslands nested in such areas successfully. However, Grange (1948) and Amman (1957) state that spring fires may destroy existing nests or remove residual cover required for nesting. Residual cover was present only in lowland areas the fire missed, whereas Sharp-tailed Grouse are typically upland nesters (Amman 1957, Hamerstrom 1939, Pepper 1972).

Instrumented females were located in the burned area several times feeding there or in immediately adjacent unburned residual or shrub cover. Numerous sightings of unmarked birds occurred in the burned area two or three days after the fire. Fires have been suggested to have a fertilizing effect and may induce more luxuriant plant growth (Amman 1957, Kirsch and Kruse 1970). This may have attracted grouse observed there in May but would not be a factor influencing the sightings immediately following the fire.

I examined sites grouse used immediately after the fire and saw no obvious differences in plants available for food. Current growth was sparse in burned and unburned areas. The fire may have increased the availability or accessibility of insects. Stoddard (1963) noted that Bobwhite (Colinus virginianus) were attracted

to insects in areas burned. Large numbers of American Robins (Turdus migratorius) foraging in the burned area in the days immediately following the fire support this idea.

Incubation

Nests

Most nests were located within one km of an arena which is similar to findings of others (Hamerstrom 1939, Symington and Harper 1957, Pepper 1972). However, they were not always nearest the arena on which the female was captured. Christenson (1971) reported that an instrumented female Sharp-tailed Grouse nested near an arena other than the capture site as did Robel et al. (1970) in the Greater Prairie Chicken.

Renests were over 200 m from the original nest sites. One female was located near her first nest site several times prior to initiation of her second clutch. Females may return to sites where first nests were destroyed because of the available nest cover which first attracted them. However, renests are located some distance away due to the presence of destroyed eggs or flattened cover at the first nest site.

The mean clutch size of eggs in my study is lower than Evan's (1968) mean of 12.0. If first nests only are used to calculate clutch size then my results agree with

Evans (op. cit.), as does hatching success (see also Hamerstrom 1939, Hart et al. 1953, Pepper 1972).

Hatchability was substantially lower (see Hamerstrom 1939, Pepper 1972), due to including a nest where only five of 10 eggs hatched. If this nest is excluded then the hatch approaches the level reported by others.

The large number of unhatched eggs in the one clutch is difficult to explain. Lance and Watson (1977) found that two instrumented female Red Grouse hatched only four of seven eggs each and suggest this resulted from instrumentation affecting the birds' behavior. Brown (1967) reported hatchability of 98% in instrumented Sharp-tailed Grouse. As low hatching success occurred at only one nest, I do not believe instrumentation affected hatchability.

The female which hatched half her clutch was a Group II bird and may have mated with a subordinate male. Such males probably have lower sperm counts (see Eng 1963. Nitchuk 1969) and fertilization could have been incomplete. Alternatively, copulation is often interrupted by males (Robel 1970, Robel and Ballard 1974) and sometimes females (Schwartz 1945).

The egg-laying rate I recorded is comparable with that of other tetraonids (Lehmann 1941, Patterson 1952). It is not known for Sharp-tailed Grouse although Johnsgard (1973) suggests it is about one a day. The incubation period has been reported ranging from 21 to 25 days (Bent

1932, McEwen and Brown 1969, Lembury in Johnsgard 1973) and my results (23-24 days) are within this range.

Nest Site Habitat

All nests were beneath overhead cover. In brushland and forest, overhead cover (shrub, tree, log) is present at most nests (Hamerstrom 1939, Edminster 1954, Pepper 1972), whereas in grasslands dense residual cover is selected (Blus and Walker 1965, Christenson 1971, Sisson 1975). Plant species composition at nests and sample plots was similar. Evans (1968) concluded that structure rather than species composition influences site selection. Recent studies support this idea (Pepper 1972, Caldwell 1976, Sisson 1975). Hamerstrom (1939) noted that a mixture of plant species was selected for nest sites when available and such was the case in this study. Species composition may be an indicator of micro-habitat selected and possibly required for successful nesting.

Residual cover height was similar at nests and sample plots, although others (see above) have suggested it is significant in nest site location. At sites where it was absent leaf litter was present, especially at nests in open forest glades. The presence and depth of litter is important to some ground nesting prairie birds (Tester and Marshall 1961). I only noted its presence or absence and generally found it only at woodland sites.

Presence of tall residual cover or litter is not the most significant factor in nest site selection in this area.

Height of the current season's grass and forb growth was similar at nests and sample plots. However, nests did have greater densities of woody stems, and shrubs were taller there. When nest sites were first selected (in mid-May) shrub stems would be one of the few forms of cover present. Pepper (1972) believed woody stems were an important component of nesting habitat, and Caldwell (1976) found 81% of nests were in low shrub cover.

In grasslands the height of the major plant species at nests is important (Christenson 1971, Wallestad and Pyrah 1974). At Chatfield the low density and height of residual cover and lack of current growth when nests are initiated results in females choosing woody stems as an alternate screening mechanism against predators. Sharp-tailed Grouse in grasslands select woody nesting cover when residual grass cover is inadequate (Kohn 1976). Grass and forb production is low in parklands as compared to grasslands (Bailey and Wroe 1974) and the residual cover they provide the following year would be less than that of grasslands. Females, therefore, probably select sites in shrubs as they offer the best cover available. Most nests had a northern exposure as suggested by Blus and Walker (1965). Bobwhite orient their nests as a negative

reaction to prevailing winds or the sun's location during the hottest part of the day (Klimstra and Roseberry 1975). Sharp-tailed Grouse nests with a north exposure, and hence overhead cover on the remaining sides would be shaded most of the afternoon. Overhead cover also protects them from predators and may be especially important in screening eggs when nests are unattended (Dwernychuk and Boag 1972).

Cover board and percent penetrated light quantified cover afforded by vegetation at nests. Measurements were taken after hatching and vegetation had changed greatly since nests were initiated, giving greatly inflated cover readings. However, Pepper (1972) suggested they are still indicative of the quality of sites and therefore useful for comparing areas. Nest sites are probably selected for the cover the site provides at the time of site selection. The proximate stimulus is likely the density of low shrub cover. Such sites are bound to have greater cover than other sites once the leaves appear on shrubs.

Movements of Incubating Females

Little is known about movements of female Sharp-tailed Grouse during the incubation period. I found them very attentive with most absences from nests occurring in the evening. Caldwell (1975) found females spent over 95% of the day on the nest. Females usually leave the nest

for a morning and evening period to feed (Hart et al. 1950, Artmann 1970) although Maxson (1977) noted that female Ruffed Grouse were absent two to five times each day. McCourt et al. (1973) suggest that the differences in nest attentiveness may be related to the proximity, quality and quantity of food during incubation. Females I located away from nests were always within 150 m of them (see also Artmann 1970). Amman (1957) and Symington and Harper (1957) suggest that nest sites may be selected initially near an abundant supply of food, a point I have already discussed.

Females were often located 3-5 m from nests and may have been birds returning to nests or leaving to forage. However, monitoring showed these birds were usually sedentary, and such observations mainly occurred near mid-day on rainy days. Females may travel only short distances during inclement weather to feed, possibly reducing the time spent away from the nest. Also, by feeding at mid-day on such days, the eggs would be exposed to otherwise cool temperatures during the warmest part of the day.

Nests situated near stands of dense cover have been reported by Bent (1932), Bernhoft (1969), Pepper (1972) and in this study. Females I flushed from nests "feigned injury" or performed distraction displays (see also McCourt et al. 1973). This probably serves to draw mammalian predators away from the nest and the nearby dense cover acts as escape cover for the female. In

grasslands, Prairie Chickens flushed from nests "feigned injury" for a short distance and then flew 0.5 km or more from the nest (Schwartz 1945). By nesting near dense cover female Sharp-tailed Grouse would require only short flights that conserve energy, a valuable commodity during incubation. Caldwell (1976) has shown that females operate at an energy deficit during incubation.

Various habitats are used by females when away from their nests. However, all feeding birds were observed in grasslands or grass-shrub areas. Crop contents of an incubating female contained mainly Lathyrus, Thalictrum, and Taraxacum, all of which are common to "prairie" areas in spring (Budd and Best 1969). Taraxacum and Lathyrus are known spring foods (Grange 1948, Jones 1966) and the leaves of Lathyrus are high in protein in spring (Campbell et al. 1966).

Incubating females appear to feed selectively on high energy foods. The short foraging periods each day demand abundant food close to the nest. Numerous clocker droppings and observations of birds in the same areas repeatedly suggest use of the same feeding site. This is supported by McCourt et al. (1973) and Maxson (1978) in other tetraonids. Therefore nest sites appear to be placed near a supply of high energy food, good escape cover and where the nest itself is suitably protected by the cover provided by vegetation.

Post-nesting Home Range and Movements

Brood-rearing Females

Home ranges of females with broods were smaller during the first two weeks of brood-rearing. This agrees with Artman (1970) and Kohn (1976), but Christenson (1971) reports ranges more than twice the size I found. Dependence on females for brooding may result in the small home ranges I observed at this time. Females with broods did not use the same sites in their home range repeatedly, but remained in an apparently defined area. Schladweiler (1965) and Godfrey (1975) suggest Ruffed Grouse broods of a similar age have no well defined range and undergo "preliminary wandering" in search of a suitable area.

Early workers suggest broods move only short distances from the nest for a week or two after hatching (Hamerstrom and Hamerstrom 1951, Uhlig and Hamor 1964, Kohridger 1965). I found movements were short, but the birds moved away quickly from the area near the nest after hatching. Christenson (1971) also reported short daily movements in young broods.

The movements I recorded are probably influenced by several factors including the availability of food, shelter, and weather. Periodic brooding of young grouse chicks is required (Koskimies 1962) and cool or wet weather may increase the time spent brooding (Cartwright 1944, Boag 1966). This would reduce foraging time per

day and therefore the distances moved. Zwickel (1967) suggested brooding periods are rhythmic and independent of weather in Blue Grouse. However, this species lives in areas of abundant rainfall and populations may have adapted to wet conditions.

Cool, wet weather in both years of this study may have affected movement patterns. Such weather has been implicated in reducing movements and foraging time (see above). The evidence available on the affects of wet weather on broods is clearly controversial and incomplete. However, I suggest wet weather reduced daily distances moved by young broods in this study.

The female I observed remaining at the nest after hatching and brooding chicks there is unusual and was probably induced by cool rainy weather. Schwartz (1945) noted that Greater Prairie Chicken leave the nest eight to 24 hours after hatching whereas Lesser Prairie Chicken remain less than four hours (Lehmann 1941). Caldwell (1976) found that young Sharp-tailed Grouse did not develop a good metabolic response to cold until 18 hours after hatching. Brooding the young near the nest after leaving it may have resulted from the chicks becoming wet from moving through wet vegetation.

I found the daily movement pattern of broods less than two weeks old similar to Christenson's (1971) study, except for the ages of young involved. Broods less than two weeks old did not move to open areas until well after

sunrise, with females brooding young at night roosts until this time. Maxson (1977) found that Ruffed Grouse broods did not reach a peak of activity until one to three hours after sunrise and suggests this is due to cool morning temperatures and wet vegetation caused by dew.

Home ranges were larger for females with chicks older than two weeks. Grassland Sharp-tailed Grouse home ranges for this period are larger (Christenson 1971, Kohn 1976) whereas in brushlands my results are comparable to Artmann's (1970). The smaller ranges used in brushlands may be influenced by the diversity of habitats available over a small area. Distances moved between feeding and resting sites may therefore be reduced.

Females moving broods to their summer range probably produced the long daily movements in broods three weeks old. Godfrey (1975) suggests that long daily movements of Ruffed Grouse broods take place when broods are "learning" their home range. In Sharp-tailed Grouse this and changing food requirements of the young as well as possible changes in availability (see Bernhoft 1969, Pepper 1972) may affect movements. As broods become established on summer ranges and become familiar with dusting, feeding and roosting areas, daily distances moved decrease. Home ranges consist of several preferred sites that are used repeatedly. These sites may be some distance apart and are interspersed with areas only used occasionally or that serve as travel

routes.

I found that early brood home ranges are rarely included in the summer range, and this is supported by Wallestad's (1971) study of Sage Grouse broods. In my study, the abandonment of the early brood range may be related to increased mobility of the chicks as they mature as well as changing diet.

Broodless Females

Broodless females used home ranges smaller than the summer ranges of brooding birds. Broodless females could probably meet their food requirements in a smaller area than females with broods, that must find food for several chicks as well as themselves. The changing diet of the young compared to the relatively constant diet of females (Grange 1948, Jones 1966) would affect home range size and movements. Schladweiler (1965) and Maxson (1978) found that broodless female Ruffed Grouse had smaller home ranges than brood-rearing birds.

Home Range Overlap

Only slight overlap in brood home ranges occurred in this study, and where it occurred there was no mutual occupation of space. Aggressive encounters were not observed. Overlap has been reported in Ruffed Grouse (Godfrey 1975, Maxson 1978) but Godfrey (op. cit.) found no mutual occupation of space and suggests behavioral

mechanisms produce this separation. Keppie (1977) found that brood mixing sometimes occurs in grouse, inferring that spatial separation is not always maintained. Home ranges established during pre-incubation when aggressive levels are probably higher (see Herzog and Boag 1977) distribute females throughout available habitat and during brood-rearing all should have a home range. Therefore, if the same range is used throughout the breeding season overlaps should be rare. Fig. 29 suggests that although the pre- and post-incubation ranges overlap they are not identical. Thus, other factors must maintain the mutual exclusion and low incidence of home range overlap.

I observed only one broodless female with another broodless Sharp-tailed Grouse. Christenson (1971) noted broodless females together several times. Hart et al. (1953) suggests females without broods begin flocking in late summer. The frequency of flocking or forming groups may be greater than I recorded as I attempted to locate birds without flushing them.

If broodless females do not aggregate, as suggested by others (Robel et al. 1970, Zwickel 1973), and brooding and broodless females do not come in contact, then some mechanism must maintain the separation; aggression has been questioned (Herzog and Boag 1977). The hypothesis put forward above, that home ranges established during pre-incubation are maintained, was tested. Fig. 30 shows that only a very small part of the pre-incubation range

Figure 29. Pre-incubation (broken line) and post-nesting (solid line) home ranges of a brood-rearing female (4107).

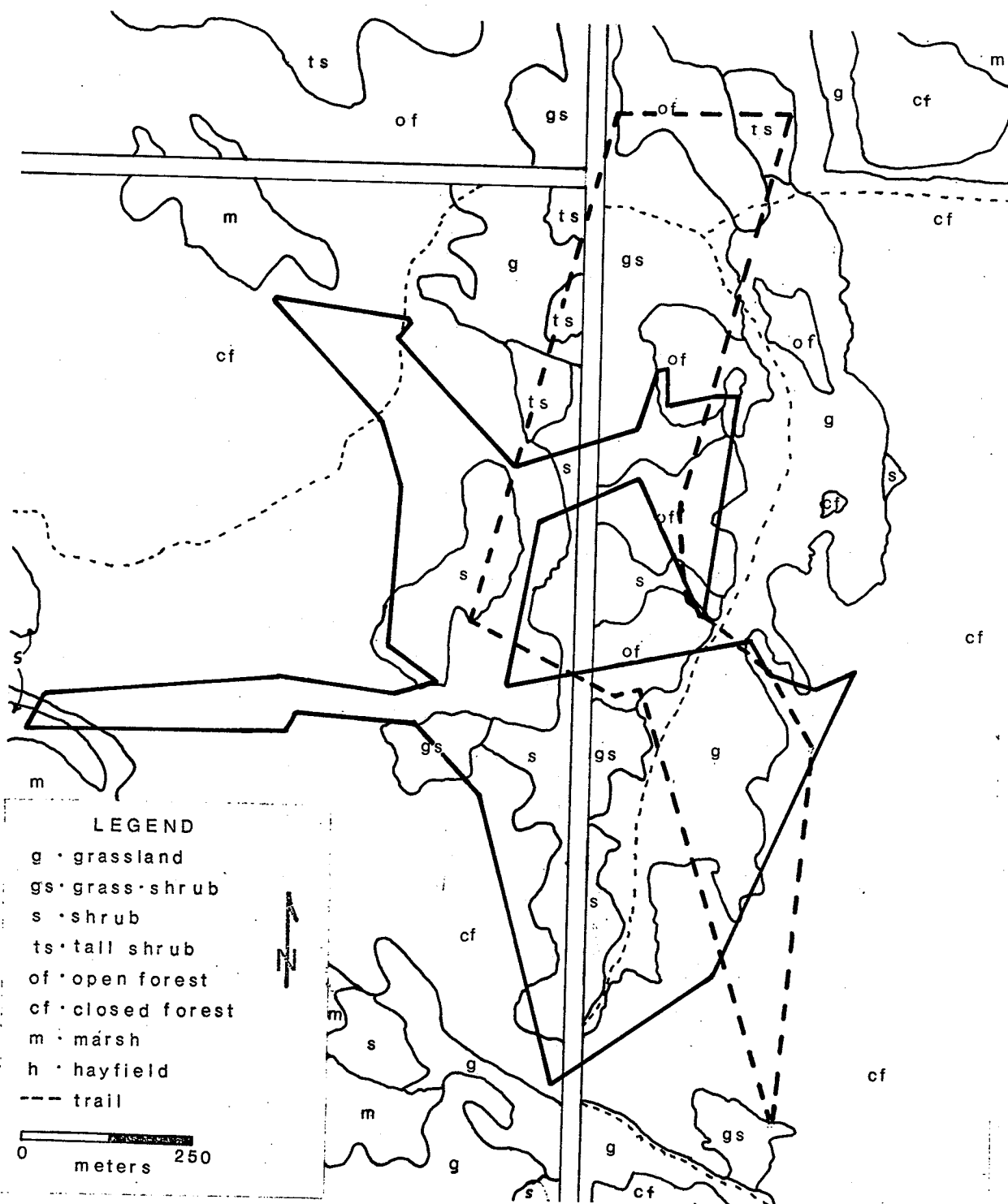
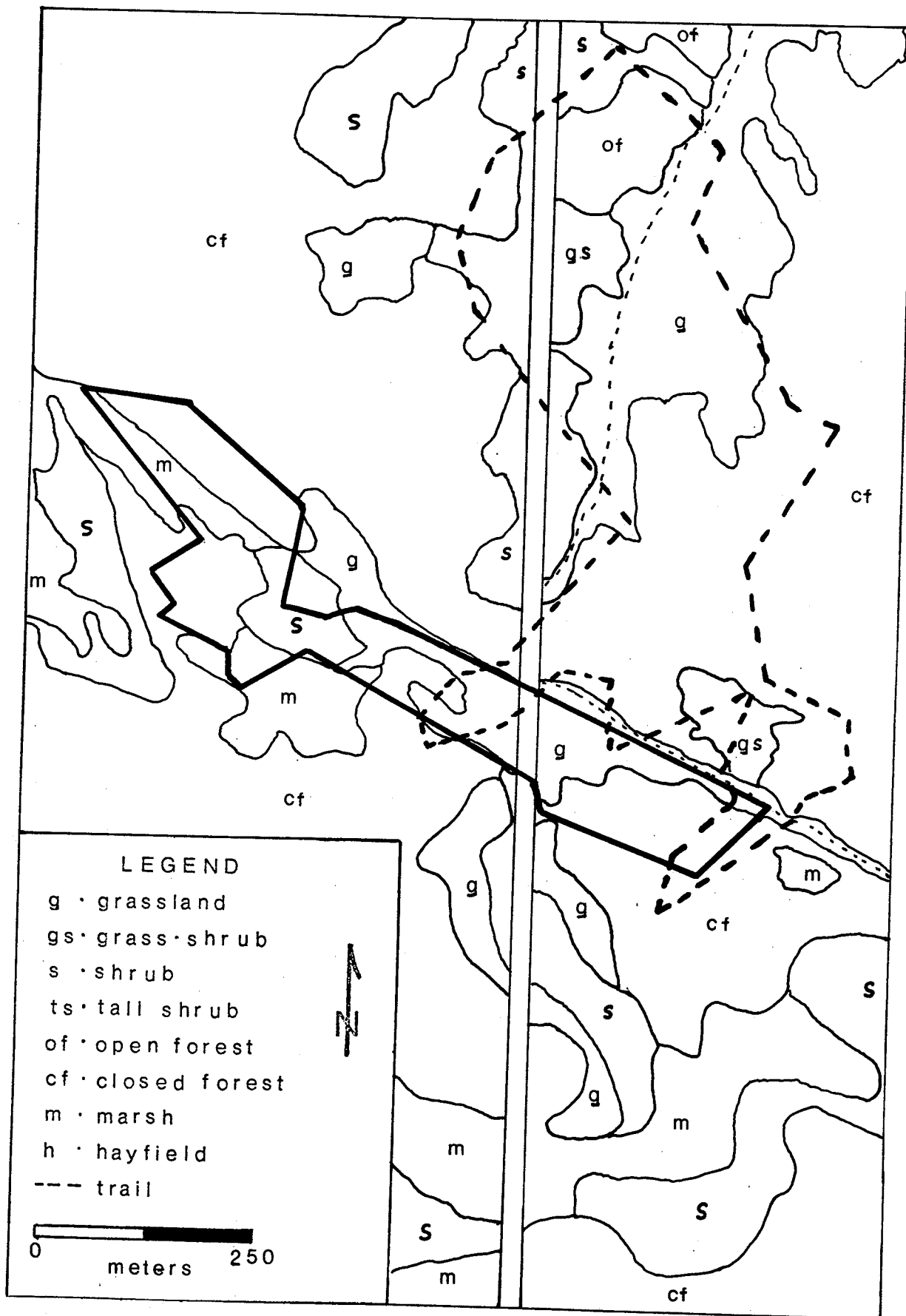


Figure 30. Pre-incubation (broken line) and post-nesting (solid line) home ranges of a broodless female (4109).



falls in the summer range. Therefore mutual occupation is prevented by some other means and aggressive interactions should not be completely ruled out.

Late Summer Shift in Home Range

The shift in home range I recorded in 1976 probably reflects the deterioration of habitat due to unusually dry weather that year. Brown (1966) and Hart et al. (1953) recorded shifts in home ranges of broods in late summer. The new home ranges were smaller, as suggested by Wallestad (1971). This may be related to reduced areas of quality habitat that remained or changing brood requirements. It may also reflect compression of home ranges as several broods move into the same area or into areas already being used by other broods.

The overlapping ranges in the new area used by two of the brood rearing females is interesting. The female which first established her new home range in the area continued using the overlap area whereas the female that arrived there several days later did not, after the initial overlap. The first female by being established there would have an advantage in any aggressive encounters, although none were observed. Aggression may increase when several broods are forced into small tracts of suitable habitat.

Post-nesting Habitat Use

At Chatfield the grass-shrub habitat, used extensively by broods, contained a variety of grasses, forbs and shrubs and would provide broods with food and cover in close proximity. This habitat is therefore preferred. Baumgartner (1939), Hamerstrom (1963) and Uhlig and Hamor (1966) report use of similar habitat by broods.

Use of grasslands was not substantial but was greater than its availability. Hamerstrom (1963) found only 14% of broods observed were in grasslands. Use of hayfields is reported (Kobridger 1965, Pepper 1972) but I found they were rarely used. This may be due to their scarcity in the study area and the greater availability of sites with native grasses and forbs. Reduction of native grass stands can affect distribution and habitat use of broods and increase use of hayfields (Pepper 1972, Sisson 1975). Broods often use brushy draws in grasslands (Aldous 1943, Bernhoft 1969) and Hart et al. (1953) found increased use of such areas as summer progressed. I found that the same habitat types were used throughout the summer. This may indicate that females with broods have available to them food and shelter in abundance and no change in habitats selected is required to meet the needs of the developing young.

Forest habitat was used 20% of the time during brood rearing. Its use has received much attention but

results are controversial. Peterle (1954) and Amman (1957) noted extensive use of wooded areas by broods. Alternately, Hamerstrom (1963) noted it is only occasionally used by broods, as did Moyles (1977). It is known that broods are more difficult to locate and flush in dense vegetation (Baumgartner 1939) and this may bias earlier studies that were dependent on flushed birds to denote habitat use.

I observed broodless females using forest and shrub habitats most often and seldom using grasslands. Habitats used by broodless females are poorly documented. Baumgartner (1939) suggests they use dense shrub thickets and Moyles (1977) found that those without broods (males and females) used dense shrub or forest most often. Forest and shrub habitats were abundant in the study area and probably not limiting in most home ranges. Therefore no change in distribution of broodless females would be expected once birds were on summer home ranges and therefore no aggregation of females as suggested by some authors occurred.

Non-use and possible avoidance of the sapling habitat by brooding and broodless females is notable. Artmann (1970) and Godfrey (1975) suggest that habitats may be selected or avoided depending on the ease with which grouse can move through them. The sapling habitat in this study was mainly aspen saplings which were very dense in most stands. Brooding females may avoid these

areas as maintaining the brood's integrity while passing through them could be a problem. All females likely avoid these areas due to difficulty in walking through them in spite of the protective cover they may afford.

The marked difference between habitats used by brooding and broodless females may also be related to differences in their food requirements. Insects, mainly grasshoppers are the main food of chicks (Criddle 1930, Pepper 1972, Sisson 1975) and are most abundant in grasses (Uvarov 1963). Adults feed mainly on forbs (Grange 1948, Jones 1966). The diet requirements of broodless females may be met more efficiently in denser cover where forbs are abundant and less likely to dry out in summer. Broodless females make only occasional excursions for short periods into open areas whereas broods use them extensively and remain there longer. Broods would require more foraging time because chicks are inexperienced and also, must pursue active prey. A female with a brood may have to move through a variety of habitat types to meet the requirements of the chicks as well as herself.

The difference in habitats used during the day is probably related to changing food availability and cover requirements. Microenvironment may be important in selection of habitats as temperature and humidity can determine the distribution and behavior of insects (Patton, 1963, Uvarov 1966). Jones (1963) and Stiven

(1961) suggest that presence of insects does not mean they are accessible. Therefore, energy derived from foraging may not exceed energy expended. Foraging periods are probably determined to some degree by the availability of insects at least for broods.

Cover board readings substantiate the hypothesis that there is a variation in cover selected over the day. Use of dense mid-day cover has been documented by several authors (Baumgartner 1939, Hart et al. 1953, Evans 1968). Of interest is cover at night roosts; sites used repeatedly. They are usually in cover denser than found at feeding sites (see also Sisson 1975) or mid-day resting areas. High cover values of sites used at sunrise and near sunset are the result of females brooding young at night roosts at these times. These results are contrary to Pepper's (1972) conclusions. He suggests open areas are used at dawn and dusk although his data shown greatest use of open areas at 18:00 hr - 19:00 hr in evening and higher cover values from 20:00 hr on.

The difference in temperature at brood locations and ambient temperature is noteworthy. Hunt (1974) found that temperature affected the use of shaded and unshaded sites by Gray Partridge (Perdix perdix). Temperature of brood sites selected may directly affect the survival of young (Lehmann 1941). The moderating effect of tall vegetation on ground temperature beneath it has been documented (Wolfe et al. 1949). Females rearing broods seem to select

mid-day resting sites in particular in relation to the site temperature as well as the cover available.

Brooding behavior is important in maintaining body temperature of young Galliformes (Ricklefs 1974). Females I studied seem to choose habitats which will offer protection for themselves and broods, from the elements as well as predators during periods of brooding. Also, these habitats may function as moderating factors on environmental extremes at such times. Although Sharp-tailed Grouse older than two weeks probably require little brooding, (Caldwell 1976) this behavior may still be important in drying chicks or helping them retain body heat under wet conditions. This is verified by observations of females brooding older chicks during rainstorms and on mornings with heavy dew.

Species composition of sites used by brood rearing and broodless females show only slight differences in sites selected. Use of denser shrub areas by broodless females confirm Baumgartner's (1939) suggestions. Shrub species at sites indicate broodless females use some lowland sites although this was not confirmed by grass and forb composition. Brooding females use sites with more upland species, or those common to edges (Maini 1968, Moyles 1977). Pepper (1972) found broods used edges also. The differences in species composition may reflect the different habitat requirements of the two groups of females.

Habitat types used during post-nesting seem to be related to the status and therefore requirements of the birds. Broodless females appear to meet their food and cover requirements in relatively dense cover and rarely use open areas. Females with broods must meet the changing requirements of the young as well as themselves. This results in a more variable habitat use pattern.

Late Summer Shift and Habitat Use

The late summer shift in home range by brood rearing females was probably the result of extremely dry conditions and their affect on vegetation. Young grouse and females feed on forbs during late summer (Bernhoft 1969, Pepper 1972) as well as insects. Insects especially grasshoppers require green grass for food (Dadd 1963) and are severely affected by combinations of high temperature and low humidity (Uvarov 1966). The dry conditions present would reduce the availability of required food items in upland sites. They would also reduce the cover provided by forbs, which may be important (see Mussehl 1963). Females with broods would have to seek alternate feeding areas in their home ranges or move to new ranges where habitat conditions are more suitable for rearing broods.

Forested areas and lowlands had succulent vegetation present well into late August. Broodless females had such habitats present in large tracts in their home ranges and

did not have to move in search of food or cover. The new home ranges of brood rearing females were associated with denser cover and lowland areas in some cases marshes were present. Brown (1966) reported a change in habitats used by Sharp-tailed Grouse under similar conditions. He found they moved from grasslands to shrubby areas as the vegetation at the former sites became desiccated (see also Wallestad 1971).

Summer habitat use is probably related to the requirements of the female and brood or female alone in broodless birds. These include food and shelter from environmental extremes or predation. Whereas these are usually available within the home ranges of each bird or brood, unusual situations may result in changes in home range location to meet these requirements.

CONCLUSIONS

Pre-nesting home range and movement patterns indicated that two groups of females existed. The movement patterns of one group suggest that a segment of the population disperses at or near the onset of the breeding season. Whether these females are less aggressive or are young birds was not conclusively determined. The movement patterns did show that females are not members of discrete subpopulations situated around one particular arena. The shift in habitat preferences shown by all females during pre-nesting is probably the result of changing diet or food availability. It may also be related to nest seeking activity.

Analysis of nesting habitat showed the sites are selected in dense stands of shrubs in otherwise open habitats (grass-shrub). Nests were located near forest or dense shrub areas, which acted as escape cover for females flushed from nests. Movement patterns of females during incubation indicated that nests are located near feeding areas. The proximity of a high quality food supply may be more significant in nest site selection than previously suspected.

The difference in home range, movement patterns and habitat use by females with broods less than two weeks old, compared to older broods is probably the result of the changing diet of chicks as they mature. Differences in home range size and habitat use by brood-rearing versus broodless females also reflects the difference in food requirements of the two groups. Larger home ranges of brood-rearing females would be required to feed the brood consisting of several birds, whereas a lone female can meet her requirements in a smaller area. Also, the more varied and changing diet of an adult with a number of chicks compared to the more constant diet of a lone female would require different habitat use by the two groups.

In general, home range and movement patterns indicate females space themselves, throughout preferred habitats, during the entire breeding season with little overlap in home range. Habitat types were not used in proportion to availability, at any time during the breeding season, suggesting females are selecting particular habitats for different activities.

RECOMMENDATIONS

- (1) A year-round study of habitat use by males and females should be undertaken. It should extend over several years to account for atypical aspects of weather or vegetation that could occur in one year (example 1976). A complete knowledge of habitat use is essential before any habitat management program can be initiated.
- (2) The home range movement study should be continued to determine the significance of dispersal, which segment of the population is involved and if it occurs annually or as a result of population levels. Also, knowledge of the area (home ranges) required by individuals throughout the year is essential in order to determine the size of land units that can successfully be used to manage a population of Sharp-tailed Grouse.

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APPENDIX 1. Female Sharp-tailed Grouse instrumented
during 1976 and 1977, Chatfield, Manitoba.

Transmitter Number	Period Tracked (Days)	Status (on Last Day Tracked)
1976		
1911	24 April - 3 June (40)	Signal lost ¹
1912	24 April - 27 April (3)	Predation ²
6489	24 April - 2 June (39)	Predation ²
4102	10 May - 13 August (95)	Study ended
6487	29 May - 13 August (76)	Study ended
-06	31 May - 6 June (6)	Predation ²
6493	7 June - 13 August (67)	Study ended
4101	8 June - 13 August (66)	Study ended
6490	2 July - 13 August (42)	Study ended
1933	11 July - 13 August (33)	Study ended
-06B	21 July - 12 August (22)	Signal lost ¹
1977		
4104	24 April - 31 May (38)	Predation ²
4106	25 April - 27 April (2)	Predation ²
4101B	26 April - 14 May (18)	Predation ²
1-8.4	26 April - 21 June (56)	Predation ²
4107	26 April - 10 August (106)	Signal lost ¹
4105	27 April - 12 August (107)	Study ended
4106B	28 April - 9 May (11)	Predation ²
4109	28 April - 26 July (89)	Signal lost ¹
6492	1 May - 13 June (43)	Signal lost ¹
4103	3 May - 13 May (10)	Predation ²
6486	4 May - 17 May (13)	Predation ²
6484	4 May - 6 May (2)	Signal lost ¹
6486B	22 May - 12 August (82)	Study ended

¹After extensive searching, the radio signal could not be located.

²Remains of bird located.

APPENDIX 2. Principle plant species found in habitat
types in the Chatfield study area.

HAYFIELD

Agropyron intermedium
Trifolium hybridum L.
Melilotus officinalis (L.) Lam.
Medicago sativa L.

GRASS, GRASS-SHRUB, SHRUB (Not all species are present
in each habitat)

Juniperus horizontalis Moench.
Bromus ciliatus L.
B. inermis Leyss
Schizachne purpurascens (Torr.) Swallen
Poa pratensis L.
Agropyron repens (L.) Beauv.
A. trachycavium (Link) Malte var. glaucum (Pease + Moore) Malte
A. trachycaulum var. novae-angliae (Seribn.) Fern.
Hordeum jubatum L.
Koeleria cristata (L.) Pers.
Oryzopsis asperifolia Michx.
Stipa spartea Trin.
Muhlenbergia glomerata (Willd.) Trin. var. cinnoides (Link) Herman
Phleum pratense L.
Spartina pectinata Link
Andropogon gerardi Vitman
Setaria viridis (L.) Beauv.
Carex spp.
Allium stellatum Fraser
Lilium philadelphicum L.
Sisyrinchium montanum Greene
Cypripedium calceolus L.
Populus tremuloides Michx.
Salix spp.
Betula glandulosa Michx.
Comandra richardsiana Fern.
Rumex occidentalis Wats.
Chenopodium rubrum L.
Anemone patens L. var. wolfgangiana (Bess.) Koch
Thalictrum venulosum Trel.
Heuchera richardsonii R.Br.
Rosa woodsii Lindl.
R. acicularis Lindl.
Fragaria vesca L. var. americana Porter
Geum triflorum Pursch

Appendix 2. Continued

Potentilla anserina L.
P. arguta Pursh
P. fruticosa L.
Rubus idaeus L.
Prunus virginiana L.
P. pensylvanica L.f.
Amelanchier alnifolia Nutt.
Trifolium repens L.
Melilotus officinalis (L.) Lam.
Oxytropis splendens Dougl.
Astragalus striatus Nutt.
Vicia americana Muhl.
Lathyrus achroleucus Hook.
L. venosus Muhl. var intonsus Butt + St. John
Linum lewisii Pursh
Polygala senega L.
Rhus pradicans L.
Eleagnus commutata Bernh.
Shepherdia canadensis (L.) Nutt.
Zizia apteria (Gray) Fern.
Arctostaphylos uva-ursi (L.) Spreng.
Apocynum androsaemifolium L.
Asclepias ovalifolia Dcne.
Lithospermum canescens (Michx.) Lehm.
Monarda fistulosa L.
Castilleja coccinea L. (Spreng.)
Galium boreale L.
Symphoricarpos occidentalis Hook.
Lonicera dioica L. var. glaucescens (Rydb.) Butters
Campanula rotundifolia L.
Liatris ligulistylis (Nels.) K. Schum.
Solidago canadensis L. var. gilvocanescens Rydb.
S. hispida Muhl.
S. rigida L.
Aster spp.
Erigeron asper Nutt.
Antennaria campestris Rydb.
Rudbeckia serotina Nutt.
Helianthus maximiliani Schrad.
Gaillardia aristata Pursh
Achillea millefolium L.
Artemesia frigida Willd.
A. ludoviciana Nutt. var gnaphalodes (Nutt.) T. + G.
Senecio spp.
Cirsium arvense (L.) Scop.
C. drummondii T. + G.
Taraxacum officinale Weber
Sonchus arvensis L.
Agoseris glauca (Nutt.) Greene
Hieracium umbellatum L.

Appendix 2. ContinuedTALL SHRUB, OPEN AND CLOSED FOREST(Not all species present
in each habitat type)

Picea glauca (Moench) Voss
Juniperus horizontalis Moench
Bromus ciliatus L.
B. inermis Leyss
B. pergans (Torr.) Swallen
Poa pratensis L.
Agropyron repens (L.) Beauv.
A. trachycaulum (Link) Malte
Elymus canadensis L.
E. interruptus Buckl.
Muhlenbergia glomerata (Willd.) Trin.
Calamagrostis canadensis (Michx.) Nutt.
Spartina pectinata Link
Setaria viridis (L.) Beauv.
Carex spp.
Lilium philadelphicum L.
Smilacina stellata L. (Desf.)
Cypripedium calceolus L.
Populus balsamifera L.
P. tremuloides Michx.
Salix bebbiana Sarg.
Salix spp.
Corylus americana Walt.
C. cornuta Marsh.
Betula glandulosa Michx.
Quercus macrocarpa Michx.
Qnemone canadensis L.
Thalictrum venulosum Trel.
Ribes hirtellum Michx.
Rosa acicularis Lindl.
Fragaria vesca L. var. americana Porter
Potentilla fruticosa L.
Rubus idaeus L. var. strigosus (Michx.) Maxim.
R. pubescens Raf.
Prunus virginiana L.
P. pensylvanica L.f.
Crataegus chrysocarpa Ashe
Amelanchier alnifolia Nutt.
Vicia americana Muhl.
Lathyrus venosus Muhl.
Rhus radicans L.
Rhamnus alnifolia L'Herf.
Viola spp.
Epilobium angustifolium L.
Aralia nudicaulis L.
Sanicula marilandica L.
Cornus stolonifera Michx.
Pyrola asarifolia Michx.
Gentiana crinita Froel.

Appendix 2. Continued

Apocynum androsaemifolium L.
Convolvulus sepium L.
Castilleja coccinea (L.) Spreng.
Pedicularis canadensis L.
Galium boreale L.
Lonicera diodica L. var glaucescens (Rydb.) Butters
Viburnum lentago L.
V. rafinesquianum Schultes
V. trilobum Marsh.
Aster spp.
Petasites palmatus (Ait.) Gray
Taraxacum officinale Weber
Hieracium umbellatum L.

MARSH

Typha latifolia L.
Scholochloa festucacea (Willd.) Link
Phragmites communis Trin.
Hordeum jubatum L.
Calamagrostis neglecta (Ehrh.) Gaertn., Mey. + Scherb.
Scirpus acutus Muhl.
S. paludosus Nels.
Carex spp.
Mentha arvensis L.