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Movements, Habitat Use, and Survival of
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MOVEMENTS, HABITAT USE, AND SURVIVAL OF RUFFED GROUSE (*Bonasa umbellus*) IN NORTHERN MICHIGAN

By

Margaret E. Clark

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ABSTRACT

MOVEMENTS, HABITAT USE, AND SURVIVAL
OF RUFFED GROUSE (*Bonasa umbellus*) IN NORTHERN MICHIGAN

By

Margaret E. Clark

The ruffed grouse (*Bonasa umbellus*) is a valued game bird throughout the United States, and northern Michigan is no exception. Declining grouse populations have met with concern by hunters and wildlife biologists. This project was initiated in 1993 to compare the movements, habitat use and survival of ruffed grouse on a site closed to hunting with those for ruffed grouse on a site open to hunting. An analysis of the composition and quality of habitat for ruffed grouse was also undertaken on the study sites. Such a comprehensive study was necessary to provide insight on the characteristics of ruffed grouse populations through fall and winter, perhaps the birds' most vulnerable times of year.

Ruffed grouse were radio-collared in the fall of 1993 and 1994, and locations were recorded for each bird several times per week to determine movements and habitat use. Dispersal movements and home ranges were similar on sites open and closed to hunting. No consistent trends were found in the movements of ruffed grouse by site, sex, or age class. Habitat use differed between sites, with birds in the open site frequently choosing

older aspen. Birds in the closed site used openings, lowland hardwoods, older pine and aspen types more frequently than expected.

Radio-collared grouse were monitored for survival through the fall and winter of 1993 and 1994. Survival between sites differed significantly in 1993, with the closed site birds having a higher survival probability. In 1994, survival was similar between sites. Avian predation was the largest source of mortality in both sites in both years, and hunting accounted for a moderate number of mortalities.

Habitat composition and quality for ruffed grouse differed between sites, with the open site having more aspen and higher quality habitat according to the Habitat Model for Ruffed Grouse in Michigan (Hammill and Moran 1986). Quality of habitat was generally lower than expected for aspen, and other habitat types met the requirements of the model as well as or better than aspen.

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INTRODUCTION

Ranging from central Alaska to the southern Appalachians, the ruffed grouse (*Bonasa umbellus*) has the most extensive distribution of any resident game bird in North America (Johnsgard 1973). It is a highly valued species throughout its range for hunting as well as nonconsumptive recreation, such as photography and bird watching. Since the early 1900s, there has been considerable attention paid to the periodic changes in the number of grouse present in the forests of North America. Still, little is known about how certain factors (e.g. seasonal movements, habitat use and hunting pressure) influence overall grouse survival. It has been recognized that a high survival rate through the fall and winter is important to future population numbers (Gullion 1970), and that several factors must play a role in determining this rate in any given year.

In the midwest, ruffed grouse generally travel several kilometers during the fall before settling in their wintering areas (Small and Rusch 1989). Fall and winter movements of grouse are assumed to be related to food supply and cover (Chambers and Sharp 1980). As the leaves begin to drop, the presence of dense vertical stems of regenerating deciduous trees, shrubs, or coniferous trees becomes important for cover (Hammill and Moran 1986). During dispersal, birds are likely to occupy less suitable habitats, at least temporarily, as they seek what they judge to be good cover (Barber et al. 1989). According to Small, et al. (1991), an increased probability of death is thought to be an inherent risk of this increased movement. Their study, in Waushara and Marquette counties in Wisconsin, showed that increased mortality during transient dispersal was negligible. However, grouse that had dispersed during the autumn season had a higher winter mortality than those that remained on an established winter range.

Providing adequate habitat may be a key to increasing the survival of birds over the fall and winter. Food and cover, as mentioned above, are the 2 factors which determine habitat quality for grouse. Because of the relatively small amount of food that is needed to sustain a grouse, it may be assumed that if a forest stand provides sufficient cover, it will have a sufficient food source as well (Hammill and Moran 1986). Habitat components which provide suitable cover from mammalian and avian predation include high stem densities, high deciduous tree and shrub height, and low conifer branch height (Cade and Sousa 1985, Hammill and Moran 1986). In Michigan, these components are principally associated with deciduous hardwood forests, especially those with aspen as a dominant species (Cade and Sousa 1985). Other habitat types which may provide suitable cover are lowland areas and young conifer stands. The amount and quality of these habitat types that is available in northern forests may help determine grouse dispersal movements in addition to affecting survival.

Hunting is assumed to be an important factor affecting fall and winter grouse survival, but its role is poorly understood. In the history of grouse hunting, management attitudes have varied dramatically, with the most recent regulations being fairly liberal (DeStefano and Rusch 1982). During the present period of increasing hunting pressure, however, there is a question as to whether the influence of humans has an additive effect on grouse mortality. Research has yet to demonstrate convincingly any impact of harvest on subsequent numbers of ruffed grouse, but there is recent evidence of high harvest rates on some public lands. Rusch et al. (1984) in Wisconsin followed the mortality of banded juveniles through the summer, and subsequent hunting season. Chick mortality through September was 63%, and another 58% of all banded grouse were lost during the harvest, October through December. The overall survival of juveniles and adults was estimated at 0.16 from hatch to December, which would require a mean hatch of 10.2 chicks per hen to balance spring production with mortality. Kubisiak (1984) also showed that high harvest rates were a potential factor depressing grouse populations at the Sandhill Wildlife Area. He emphasized that the area studied had excellent road access, exceptionally high hunter effort and a high proportion of hunters using dogs, which are also typical characteristics for many hunting areas in northern Michigan.

To comprehensively describe the fall and winter characteristics of a grouse population, each of the above mentioned factors must be detailed. With the use of radio-telemetry, there is the possibility of knowing specific causes and rates of mortality. In addition, movements and habitat use can be measured with relative ease. This study investigates survival, habitat use and movements on two large areas of land in northern Michigan. To observe these factors in combination with the effects of hunting pressure, 1 area has been closed to grouse and woodcock hunting for the duration of the project. I will describe and compare two separate grouse populations, and discuss the management implications which arise from the results of this project.

OBJECTIVES

The specific objectives of this study are to:

1) determine habitat use and movements of ruffed grouse on sites open and closed to hunting through the fall and winter;
2) determine habitat quality and quantity on study sites;
3) determine the survival probability and the causes of ruffed grouse mortality on study sites in fall and winter; and
4) relate measured variables to survival.

STUDY AREA

This study was conducted in the Pigeon River Country State Forest (PRCSF), which is located in the northern part of Michigan's lower peninsula. It comprises approximately 98,000 acres in Cheboygan, Otsego and Montmorency counties. A section of the forest was separated into two study sites, one open to all hunting under normal regulations and one closed to grouse and woodcock hunting for the duration of the study. The closed site comprises approximately 91 km^2 (35 mi^2) in Otsego county (Figure 1). Although the rest of the PRCSF is open to hunting, we have arbitrarily drawn a boundary around 124 km^2 (48 mi^2) in Cheboygan county as the open study site (Figure 1).

The area is characterized by moraines, till plains, outwash plains, lake plains and deltas, which are the results of glaciation and post glacial lakes. The dominant soil associations in the PRCSF are Cheboygan-Blue Lake, Au gres-Rubicon Roscommon, and Detour-Grevourt. These soils range from low fertility dry sands on the outwash plains to medium-high fertility sandy loams on till plains and moraines (Tardy 1991). The Black, Sturgeon and Pigeon Rivers originate on the southern edge of the area and flow northward.

The average winter temperature is -7.9 C, with an average daily minimum of -10.5 C. The summer average is 17.3 C, with an average daily maximum of 25.8 C. Total

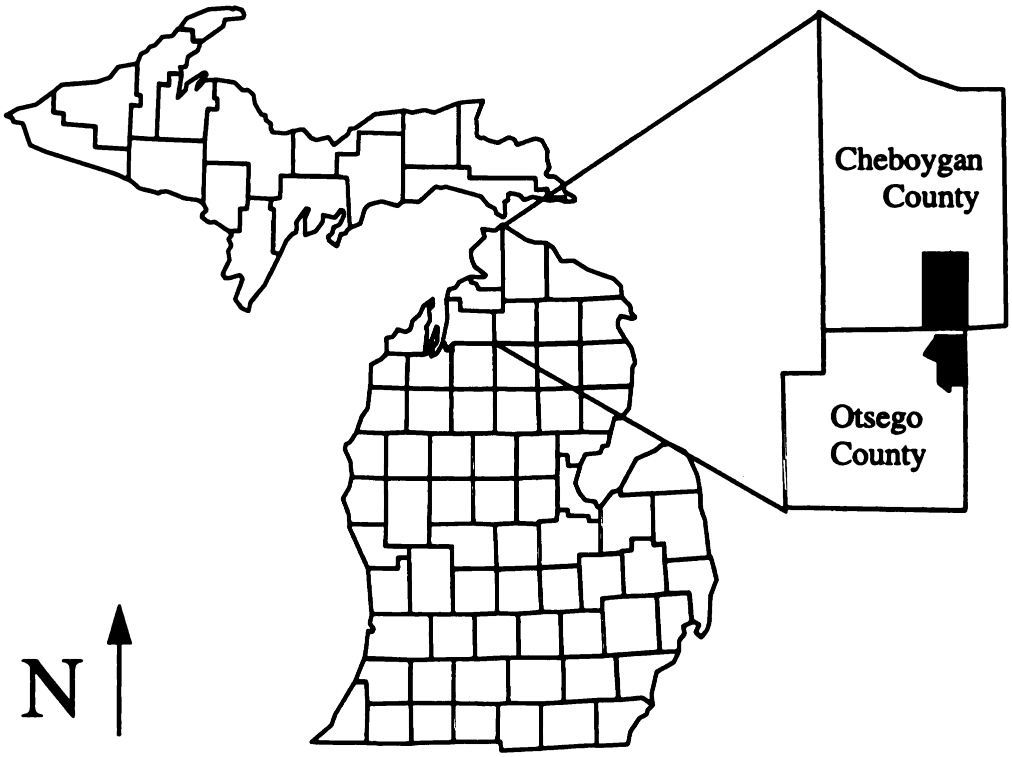


Figure 1. Location of the site open to hunting in Cheboygan County and the site closed to hunting in Otsego County, in the northern lower peninsula of Michigan.

annual precipitation is 77.4 cm, and average seasonal snowfall is 291.1 cm (Tardy 1991).

A diversity of vegetation types are present in the PRCSF. The lowland areas are dominated by white cedar (*Thuja occidentalis)*, Balsam fir (*Abies balsamea*), and alder (*Alnus* spp.). Uplands consist primarily of sugar maple (*Acer saccarinum*), jack pine (*Pinus banksiana*), quaking aspen (*Populus tremuloides*), bigtooth aspen (*Populus grandiadentata*), white pine (*Pinus strobus*) and red pine (*Pinus resinosa*).

METHODS

Trapping and collaring

Project field work began in May of 1993 and continued through May of 1995. Trapping and collaring took place in the fall of 1993 and 1994. In 1993, in the site open to hunting, trapping began on August 1 and continued through September 14 (the day before the start of grouse hunting season). In the site closed to hunting, trapping continued through October 2, in an attempt to collar an equal number of birds between sites. In 1994, birds were trapped between August 7 and October 4 in the open site, and through October 17 in the closed site. Initial trapping sites were selected based on bird sightings by Michigan Department of Natural Resources (MDNR) personnel or project personnel, or by their apparent quality as grouse habitat. Young aspen stands with dense understory vegetation were assumed to support the highest density of grouse in summer and early fall (Edminster 1947). Because of frequent grouse flushes, aspen stands in conjunction with alder and cedar swamp edges were generally selected for trapping.

Modified cloverleaf traps (Dorney and Mattison 1956) were placed in selected forest stands with an attempt to orient the traps at right angles to suspected bird movements. Each trap consisted of 4 trap bodies made of 2" x 4" welded wire and 2 50' leads made of 18" tall chicken wire. The trap bodies were covered with 3' x 3' lids, and the lids were camouflaged with ferns and other vegetation. The forest floor was cleared to approximately 6" on each side of the lead to facilitate bird movements toward the trap bodies. On the door of the trap body, chicken wire was shaped into a funnel, so that grouse could enter the trap body but not exit.

All trapping and handling procedures were approved by the Michigan State University Committee on Research Involving Animal Subjects (AUF # 10/93-400-03) before the start of the project. Grouse were sexed according to tail and rump feather size and coloration, as described by Dorney (1966), Roussel and Ouellet (1975), and Larsen and Taber (1980). Juveniles were identified by size during the month of August, and by wear on the 9th and 10th primary feathers (Godin 1960) after September 1. Weight and wing length were measured as an index of general condition. Birds weighing over 350 g were fitted with a numbered leg band, and a necklace-style radio collar which weighed approximately 11 g. Collars were equipped with an 8-hour mortality sensor, and were obtained from either Advanced Telemetry Systems Inc., Isanti, MN, or Lotek Engineering Inc., Ontario, Canada (inclusion of company name does not imply endorsement).

Birds that weighed less than 350 g, or had trapping injuries around the head and neck, were banded and released immediately. Birds that had injuries which appeared life-threatening, or interfered with their ability to walk, were euthanized by vertebral separation. Any animals other than ruffed grouse that were caught during trapping were released immediately in the safest possible manner. Radio-collared birds were located and flushed the day after trapping to ensure that there were no problems related to trapping or improper radio fitting.

Vegetation sampling

Vegetation sampling was undertaken on 2 levels. The first level compared the percentages of different habitat types in the open and closed sites in the PRCSF. There are 26 different cover types which the MDNR uses to classify state land. For sampling purposes, specific types were combined into more general categories. In addition, aspen was split into three age classes: 1 - 10 years, 11 - 29 years, and 30 + years. This resulted in a total of 9 different cover types, shown in Table 1. Compartment maps and forest inventories were used to calculate the percentage of each forest type in each site. Private inholdings are not included in the breakdown of habitat types. They comprise approximately 3 % of the open site, and 7 % of the closed site.

The second level of vegetation sampling quantified habitat quality for ruffed grouse in both sites of the PRCSF, based upon the requisites described in the Habitat Model for Ruffed Grouse in Michigan (Hammill and Moran 1986). Variables sampled correspond to habitat requirements for fall-winter cover and winter food, which are considered limiting factors in the northern range of ruffed grouse.

The fall-winter cover requirement in the model is related to 6 variables: stem density of deciduous, conifer, and shrub stems; height of deciduous and shrub stems; and low branch height of conifer stems. Between 2 and 22 stands in each habitat type in each site were randomly chosen for sampling (Table 2). Young conifer stands were very rare in the open site, resulting in only 2 stands being sampled. Because of standing water and inaccessibility, lowland conifers and lowland hardwoods were sampled with only medium intensity (4 - 8 stands). The category "Other" was not sampled, as it was assumed

Table 1. Michigan Department of Natural Resources cover type components used for each sampling category in 1994 and 1995 vegetation sampling in the PRCSF.

Sampling category	(Type code) Cover type
Aspen, 1 - 10 years	(A) Aspen
Aspen, 11 - 29 years	(A) Aspen
Aspen, 30 + years	(A) Aspen
Upland hardwoods	(B) Paper birch, (M) Northern hardwood, (O) Oak, (P) Balsam poplar
Lowland hardwoods	(E) Swamp hardwoods, (L) Lowland brush, (N) Marsh
Conifers, 1 - 30 years	(H) Hemlock, (R) Red pine, (W) White pine
Conifers, 31+ years	(H) Hemlock, (R) Red pine, (W) White pine
Lowland conifers	(C) Cedar, (D) Treed bog, (F) Spruce - fir, (Q) Mixed swamp conifer, (S) Black spruce, (T) Tamarack, (V) Bog or muskeg
Jack pine	(J) Jack pine
Other	(G) Grass, (I) Local use, (K) Rock, (U) Upland brush, (X) Non-stocked, (Y) Sand dunes, (Z) Water

Table 2. Number of stands sampled in each site and plot size used for each sampling category in 1994 and 1995 vegetation sampling in the PRCSF.

Sampling category	Number of stands sampled		Transect size (m)
	Open site	Closed site	
Aspen, 1 - 10 years	19	16	2 x 25
Aspen, 11 - 29 years	18	22	2 x 25
Aspen, 30 + years	21	18	10 x 25
Upland hardwoods	9	10	10 x 25
Lowland hardwoods	4	4	2 x 25
Conifers, 1 - 30 years	2	8	4 x 25
Conifers, 31+ years	10	10	10 x 25
Lowland conifers	4	8	4 x 25
Jack pine	7	10	4 x 25
Other[a]	-	-	-
Total	94	106	

[a]This category was not sampled.

that stem density was 0 in types such as grass, water, and rock. Because of its importance as grouse habitat in the northern United States (Bump et al. 1947, Gullion 1970), aspen was sampled with more intensity than other habitat types.

Within each stand, variables were quantified in 3 randomly placed belt transects of 2m, 4m or 10m x 25m in size (Table 1). Size of the plot varied depending on the density of the habitat type, with dense types like young aspen having smaller plots than sparse types like mature red pine.

Within each plot, stem density, average height of shrubs and trees, and average low branch height of conifers were measured. Any woody vegetation greater than 0.9 m tall was counted, and separated into the categories deciduous, coniferous, or shrub stems as called for by Cade and Sousa (1985). An equivalent stem density (ESD) was calculated for each stand using the formula:

$$ESD = d + 4c + 0.50s$$

where d = deciduous stems/ha, c = coniferous stems/ha and s = shrub stems/ha (Hammill and Moran 1986). Ten deciduous trees and 10 shrubs (by model definition) were randomly chosen, and the height of each was measured using a meter stick or a Haga altimeter. Ten conifer trees were also chosen and measured for lowest branch height. These variables are considered important for fall-spring cover, influencing predation by both mammals and avian predators.

Although not called for in the model, the woody stem category was further broken down into percent aspen in each of three size classes: seedlings, saplings and mature trees. Size class was determined using diameter at breast height (dbh): seedlings < 9 cm dbh, saplings 9 - 18 cm dbh, mature trees > 18 cm dbh. This information was used to further analyze grouse habitat, specifically in aspen stands, beyond the scope of the HSI model.

To satisfy the winter food requirement of the habitat model, a stand must contain any canopy cover of mature aspen. If it does not, then quality decreases as the distance to the nearest stand with an aspen canopy increases. In stands that lacked a winter food source, the distance from the center and edge of the stand to the nearest winter food source was measured on MDNR compartment maps.

Values for each variable in each stand were entered into the production functions of the model (Appendix I, Figure 1- 5), and an overall habitat suitability index (HSI) value was calculated for the stand, using the formula:

$$HSI = \frac{V_1(d(V_2)+4c(V_3)+0.5s(V_4))}{d + 4c + .5s} V_5$$

where V_1 corresponds to ESD index value (Appendix I, Figure 1); V_2 corresponds to deciduous tree height index value (Appendix I, Figure 2); V_3 corresponds to conifer branch height index value (Appendix I, Figure 3); V_4 corresponds to shrub height index value (Appendix I, Figure 4); and V_5 corresponds to distance between life requisites index value (Appendix I, Figure 5).

Survival and habitat use

Radio telemetry was used to monitor the survival of grouse from late summer through the following spring on each of the study sites. Radios were equipped with 8 hour mortality sensors, and birds were collected as soon as the mortality sensor was known to be active. Cause of death was determined whenever possible. Predator signs and habitat type were noted, and carcasses were collected for necropsy at the MDNR's Rose Lake facility. Mortality causes were categorized as avian predation, mammalian predation, hunting, stress/suffocation, illness, or unknown. Birds which survived for more than five days after capture were used for survival analysis.

According to White and Garret (1990), transmitter failure or the inability to locate an individual animal causes the survival time of that animal to be censored. If a bird was unable to be located after an intense ground and air search, it was considered "censored". If a bird died of stress or suffocation due to the radio-collar after 5 days after capture, it also was considered censored in the survival analysis, because the natural fate of the bird (if it had not been caught and collared) cannot be determined.

Radio locations for each bird were taken approximately every other day from date of capture through the end of December. Bird locations were estimated on topographic maps using two compass bearings from known locations, which were usually points on county roads. The radios used in this study had a fairly strong signal up to 2 km away. For accuracy, however, bearings were generally taken from less than 1 km from the location of the bird. Field trials by research personnel indicated an average bearing error of approximately 2°, which generally resulted in an error polygon of < 3 ha. The average size of a forested stand in the PRCSF is 10 hectares, so the error associated with habitat evaluation was assumed to be negligible. Universal Transverse Mercator (UTM) coordinates were transcribed to MDNR vegetation maps and compartment number, and the stand number and habitat type occupied by the bird were recorded. If a location fell on a stand line between two habitat types, the equivalent of half of one location was assigned to each habitat type. If a bird moved onto private land, Michigan Inventory Resource Information System (MIRIS) maps were used to determine the habitat type being occupied. The time of location for each bird was varied daily to provide maximum habitat use information. If a bird was located 10 or more times during the fall and winter, it was used as part of the habitat use study.

Movements

Telemetry data were also used to quantify movements of birds throughout the fall and winter. Since birds were located for a variable number of days per week, a weekly harmonic center (Dixon and Chapman 1980) was calculated for each bird using TELEM88 (Virginia Polytechnic Institute and State University, Dept. of Fisheries and Wildlife, Blacksburg, VA). If a bird was located during at least 5 different weeks between time of capture and December 31, then it was analyzed for fall movements. Weekly harmonic centers were plotted and numbered by week as a visual representation of seasonal movement. The straight line distance between the harmonic center of each week and the harmonic center of the first week located was used as a graphical analysis of movement.

These graphs, listed in Appendix II, were then used to determine whether or not birds exhibited dispersal movements. Birds which never moved more than 500 m from the first week after capture were categorized as Type I non-dispersers (Appendix II, Figure 1 and 2). Birds which moved more than 500 m from the harmonic center of the first week after capture for 1 or 2 weeks at a time, but then returned to within 500 m, were categorized as Type II non-dispersers (Appendix II, Figure 3 and 4). Fall/winter home ranges were calculated for Type I and Type II non-dispersers using the convex polygon (Mohr 1947) and harmonic mean (Dixon and Chapman 1980) methods.

Birds which moved more than 500 m from the harmonic center of the first week after capture and stayed 500 m or farther away for 3 or more consecutive weeks before November 30 were considered dispersers, or Type III (Appendix II, Figure 5 and 6). Dispersal distance was considered to be the linear distance between the center of those locations before dispersal to the center of those locations after dispersal. Because of the time of year, some birds may have been caught during dispersal, causing an underestimation of dispersal distance. If a bird was caught during dispersal, dispersal distance was considered to be the linear distance between the first location and the center of those locations after dispersal. Some birds that were caught late in the season may have finished dispersing before being radio-collared, which would result in some early dispersers being miscategorized as non-dispersers. Therefore, the number of dispersers and the distance of dispersal should be considered a conservative estimate.

Data analysis

Homogeneity of habitat types between sites (open and closed to hunting) was compared using a Chi-squared test (Siegel and Castellan 1988). Using the Habitat Model for Ruffed Grouse in Michigan (Hammill and Moran 1986), the quality of habitat was evaluated on a stand by stand basis. Mean HSI values for each habitat type were compared between areas using a Student's t-test (Rosner 1990) The quality of habitat within the sites was extrapolated by multiplying the mean HSI value for each habitat type to the proportion of that habitat type in each site.

Grouse locations through fall and early winter were used to quantify habitat use, which was compared to habitat availability using PREFER (Great Lakes Fishery Laboratory, U.S. Fish and Wildlife Service, Ann Arbor, Michigan). A habitat use value was calculated for each bird by multiplying the proportion of that bird's locations in each habitat type by the mean HSI value for that type. A mean habitat use value was calculated for each site, and sites were compared using a Kruskal-Wallis one-way ANOVA and Multiple Comparisons (Siegel and Castellan 1988). Fall and winter home range and dispersal movements in 1993 and 1994 were compared between sites using an Student's t-test (Rosner 1990). Comparisons were also made between sex and age class, and dispersal type.

Survival probabilities for the radioed birds on each site were calculated using the Kaplan-Meier Product Limit estimator. This technique provides an estimate of the survival probability at any point in the study period (Kaplan and Meier 1958). Survival probability curves were also generated for birds by age class and sex, and curves were compared using the Log-rank test (Lee 1992) provided by the program SAS (SAS

Institute, Cary, North Carolina). Selected variables were compared to survival in both the open and closed areas with the Cox proportional hazards model (Cox 1972), also using the SAS system. Percent of increase or decrease in the hazard of a particular covariate was determined by converting the risk ratio in the following manner; percent difference in hazard = 100*(risk ratio-1).

RESULTS AND DISCUSSION

Trapping

In 1993, the most productive weeks in the open site were the 6th and 7th, which had capture rates of 0.050 and 0.056 birds per trap night (Table 3). A total of 47 birds (including recaptures) were caught, of which 36 individual birds were radio-collared. Two birds were banded only (not radio-collared) due to trapping injuries, 2 were euthanized and 2 were released without being processed. In addition, there were 5 recaptures of birds which had already been radio-collared or banded.

In the closed area, week 8 was the most successful, with a rate of 0.066 birds per trap night (Table 3). Thirty-three birds were caught in the closed site during 1993, of which 28 individuals were radio-collared. Of those that were not collared, 2 were found dead in traps, killed by unknown predators. Two birds that sustained trapping injuries were banded only, and 1 bird was a recapture. During week 9 no birds were caught in 124 trap nights, possibly due to cold, rainy weather. In both years and both sites, daily trapping success was generally low if rain was present before early evening. Backs et al. (1985) found that week to week trapping success seemed to be related to prevailing weather conditions in Indiana.

Late September to mid-October is the peak of fall dispersal for grouse in Wisconsin (Small and Rusch 1989). In 1994, in the open site, trapping continued into

Table 3. Trapping results for 1993, PRCSF open and closed sites. Birds caught includes recaptures and birds not collared.

Week	Dates	Open site			Closed site		
		Trap nights	Birds caught	Birds per night	Trap nights	Birds caught	Birds per night
1	8/1 - 8/7	91	4	0.04	92	1	0.01
2	8/8 - 8/14	204	3	0.02	161	2	0.01
3	8/15 - 8/21	188	6	0.03	177	2	0.01
4	8/22 - 8/28	182	8	0.04	189	3	0.02
5	8/29 - 9/4	242	9	0.04	105	5	0.05
6	9/5 - 9/11	260	13	0.05	105	1	0.01
7	9/12 - 9/18	72	4	0.06	87	4	0.05
8	9/19 - 9/25				226	15	0.07
9	9/26 - 10/2				124	0	0.00
	Total	1239	47[a]	0.04	1266	33[b]	0.03

[a]Number includes 5 recaptures, 2 birds which were banded only, 2 which were euthanized, and 2 which were released without being processed.
[b]Number includes 1 recapture, 2 birds which were banded only, and 2 which were found dead in the trap.

hunting season so that we might make use of the increased movements of fall dispersal for trapping. Trapping did not seem to cause any problems with hunters, and vandalism was minimal. The longer trapping period and the addition of more traps resulted in more trap nights in both sites in 1994. Weeks 5, 6 and 8 were the most productive in the open site, and a total of 63 birds were captured during the trapping season (Table 4). Of these, 1 was found dead in the trap, 1 was accidentally released, 7 were recaptures and 7 were banded only. Two of the recaptures were banded only. Researchers removed the collar of one bird that was recaptured with injuries, but the bird was recaptured and recollared the following week. This resulted in a total of 47 birds collared in the open area in 1994.

Weeks 4 and 11 were the most productive weeks in the closed site in 1994, with success rates of 0.051 birds per trap night (Table 4). In week 5, there were no birds caught in 119 trap nights, although the same week was fairly productive in the open site. A total of 52 birds were captured, and 42 individuals were collared. One bird was found dead in a trap, killed and eaten by a northern goshawk (*Accipiter gentilis*) which was still in the trap when researchers arrived. Four birds were banded only, and 5 were recaptures.

Success rate was higher in the open site in both years. In general, more young aspen areas which were productive for trapping were found in the open site. The total number of birds per trap night did not change much within sites between 1993 and 1994, despite MDNR and hunter reports of higher population numbers in 1994. Overall success rate in both sites was substantially lower than that reported by other researchers. Dorney and Mattison (1956) reported success rates as high as 0.768 grouse per trap night in a small area of high grouse density. More comparable trapping efforts in Indiana

Table 4. Trapping results for 1994, PRCSF open and closed sites. Birds caught includes recaptures and birds not collared.

Week	Dates	Open site			Closed site		
		Trap nights	Birds caught	Birds per night	Trap nights	Birds caught	Birds per night
1	8/1 - 8/7	6	0	0.00	23	1	0.04
2	8/8 - 8/14	127	3	0.02	193	6	0.03
3	8/15 - 8/21	208	8	0.04	196	1	0.01
4	8/22 - 8/28	216	1	0.01	176	9	0.05
5	8/29 - 9/4	237	12	0.05	119	0	0.00
6	9/5 - 9/11	243	14	0.06	119	3	0.03
7	9/12 - 9/18	232	10	0.04	119	3	0.03
8	9/19 - 9/25	202	12	0.06	171	6	0.04
9	9/26 - 10/2	125	3	0.02	221	7	0.03
10	10/3 - 10/9	36	0	0.00	226	7	0.03
11	10/10 - 10/16	0	0		176	9	0.05
12	10/17 - 10/23	0	0		16	0	0.00
	Total	1632	63[a]	0.04	1755	52[b]	0.03

[a]Number includes 7 recaptures, 7 birds which were banded only, 1 which was found dead in the trap, and 1 which was released without being processed.
[b]Number includes 5 recaptures, 4 birds which were banded only, and 1 which was found dead in the trap.

between 1975 - 1984 had a mean annual success rate of 0.062 grouse per trap night (Backs et al 1985). The 2 year mean success rate in this study was 0.038 in the open site and 0.028 in the closed site. These years, however, were assumed to be at the lowest point of the population cycle in Michigan (John Urbain, MDNR, pers. comm.). Over a 10-year period, this number might increase with the inclusion of years with high population numbers.

The age and sex ratios of radio-collared birds did not differ significantly between sites in either year ($p > 0.10$) (Table 5). In 1993 in both sites, and in 1994 in the closed, there were slightly more adult birds radio-collared than juveniles. These results are not consistent with prior research which showed that juveniles are more susceptible to trapping with cloverleaf traps (DeStefano and Rusch 1986). The 2" x 4" welded wire that was used in making trap bodies for this study may have resulted in juvenile birds escaping early in the trapping season. It is also possible that some juveniles were mistaken for adults, due to the difficulty in aging by wing molt after 1 September (Bump et al. 1947). With the exception of the open site in 1994, the ratio of males to females approximated 1:1.

Incidental captures for both years included rabbits, raccoons, a juvenile porcupine, an opossum and a skunk. All were released safely.

Table 5. Number of birds radio-collared in the PRCSF by site, year, sex and age class. No significant differences in age or sex distributions were detected between sites or years (Chi-square, $p > 0.10$).

		Open site		Closed site	
Sex	Age class[a]	1993	1994	1993	1994
Female	AHY	9	8	7	8
	HY	10	9	7	10
	UNK	0	1	0	2
Total	Female	19	18	14	20
Male	AHY	11	13	11	12
	HY	6	11	3	4
	UNK	0	1	0	3
Total	Male	17	25	14	19
Unknown	AHY	0	1	0	2
	HY	0	3	0	1
Total birds		36	47	28	42

[a]Age class abbreviations are as follows: AHY = adult (after hatch year), HY = juvenile (hatch year), UNK = unknown (could not be determined from feather characteristics).

Habitat

Before European settlement, Michigan forests were probably a mosaic of pines and Northern hardwoods, interspersed with various sized areas of natural disturbance. These areas, filled with thick regenerating vegetation, were probably home to a variety of wildlife which depended on early successional species for food and cover. With the logging and subsequent burning of much of the state (including the PRCSF) in the beginning of this century, virtually all of the older forest types were converted to early successional species such as aspen (Leatherberry and Spencer 1996).

Bailey et al. (1955) was perhaps the first to note the similarity between the ranges of ruffed grouse and trembling aspen in North America. Over the northern part of that range, where snow cover persists for 4 - 6 months, aspen is an important part of the winter diet of grouse (Bump et al. 1947). Since the 1930's, total acreage of this vegetation type has been on a steady decline in Michigan. This decrease has been primarily due to the deterioration of aspen stands and natural succession of other forest types, predominantly hardwoods (Raile and Smith 1983).

The statistical distribution of habitat types in the open site is typical of this current trend (Table 6). In the open site, upland hardwoods predominate, comprising about 24% of the total area. Species include maple, birch (*Betula papyrifera*), poplar (*Populus balsamifera*) and a small amount of oak (*Quercus* spp.). Aspen is well represented as a species when age classes are combined (34%). However, the structural configuration of aspen changes quickly and dramatically over time, as does its quality as grouse habitat. According to Hammill and Visser (1984), the most important age class of aspen for grouse through fall and winter is < 25 years, but sapling aged aspen (1 - 10 years)

Table 6. Distribution of habitat types in the Pigeon River Country State Forest open and closed sites.

Habitat type	Open site[a] Area (ha)	Open site[a] Percent of total	Closed site Area (ha)	Closed site Percent of total
Aspen 1-10 yr.	1135	9.38	642	7.62
Aspen 11-29 yr.	1862	15.38	853	10.14
Aspen 30+ yr.	1061	8.76	590	7.02
Upland hardwoods	2861	23.63	1652	19.62
Lowland hardwoods	960	7.93	375	4.46
Pine 1-30 yr.	47	.39	284	3.37
Pine 31+ yr.	1439	11.89	1764	20.96
Lowland conifers	1774	14.65	1464	17.40
Jack pine	200	1.65	470	5.59
Other	767	6.34	322	3.83
Total area	12106		8416	

[a]The distribution of habitat types in the open site is significantly different from the distribution of habitat types in the closed site (Chi-square, 9 df, $p < .001$).

is often too dense (Gullion 1970). Eliminating the classes which are considered too old and too young, the middle and most important age class of aspen for grouse (11-29 years old) represents about 15 % of the total area of the open site. There is very little jack pine (2%) or young pine (< 1%) in the open site, because of little or no planting of these types.

The distribution of habitat types in the closed site is significantly different than in the open site ($p < 0.001$) (Table 6). The primary difference between the sites lies in the dominant species. Like the open site, the closed site does have a high percentage of hardwoods (20%), but also has about an equal percentage of pine > 30 years of age (21%). The older pine category is partially comprised of red pine or mixed pine plantations, which have been historically planted as a timber resource in Michigan. Soil types in the closed site may also be conducive to the succession of pine types, which are harvested in a 60 - 70 year rotation (Joseph Jarecki, MDNR, pers. comm.). The combined aspen age classes equal approximately 25% of the closed site, slightly less than the open site. Percentages of young pine and jack pine are slightly higher in the closed site, most likely due to planting.

The open site is fairly homogeneous with regard to the distribution of habitat types across the landscape. The closed site, however, has a distinct shift in habitat types from the northwest the southeast. This shift is hidden in the overall distribution (Table 6). Birds that were trapped in the closed site tended to stay in either the northwest or the southeast. Because of this heterogeneity, the closed site was separated on compartment lines into 2 areas, referred to as the North area and the South area (division is shown on maps in Appendix III, Figure 5 - 8). The distribution of habitat types differs significantly between the North and South areas of the closed site ($p < 0.001$) (Table 7).

The North area is 35% pine over 30 years of age, with very few aspen dominated stands. Much of the older pine that is present in the closed site is in the North area. The middle age class of aspen comprises just 7% of the area, and only 11% of the area is aspen of any age class. If clear-cutting for the regeneration of aspen stands continues at the current rate, there will be even fewer hectares of forest in the middle age class in 10 to 20 years. Aspen 1 - 10 years of age makes up just 2% of the North area of the closed site. Assuming the importance of the middle age class of aspen for grouse, it may be speculated that the amount of quality habitat is on a decline.

The South area is similar to the open site in distribution of aspen types, but is still significantly different in overall distribution ($p < 0.001$). About 36% of the area is comprised of aspen of combined age classes. Twelve percent of the South area is aspen 1 - 10 years old, indicating a high level of clearcutting in recent years. The middle age class of aspen makes up 13% of the area, about twice the percentage of the North area. Like the open site, only 10% of the South area consists of pine over 30 years of age. The South area differs from both the North area and the open site in its large percentage of lowland conifers (22%).

The amount of aspen present has been and will continue to be important for ruffed grouse in northern Michigan and the PRCSF. But although it is important to describe habitat distributions, quality of each habitat type must further be evaluated.

Table 7. Distribution of habitat types in the North and South areas of the Pigeon River Country State Forest closed site.

Habitat type	North area[a]		South area	
	Area (ha)	Percent of total	Area (ha)	Percent of total
Aspen 1-10 yr.	77	2.10	564	12.04
Aspen 11-29 yr.	250	6.66	606	12.92
Aspen 30+ yr.	75	2.04	515	11.00
Upland hardwoods	782	20.93	869	18.58
Lowland hardwoods	115	3.10	259	5.54
Pine 1-30 yr.	231	6.15	53	1.14
Pine 31+ yr.	1315	35.15	448	9.61
Lowland conifers	441	11.83	1022	21.84
Jack pine	321	8.55	151	3.22
Other	130	3.50	192	4.10
Total area	3737		4679	

[a]The distribution of habitat types in the North area is significantly different from the distribution of habitat types in the South area (Chi-square, 9 df, $p < .001$).

Habitat quality

Habitat quality within each habitat type was generally similar between the open and closed sites (Table 8). Mean HSI values of habitat types differed significantly between sites in aspen 11-29 years ($p < 0.10$) and in aspen 30 years and older ($p < 0.01$). In the open site, aspen 30 years and older had a relatively high mean HSI value of 0.495. This value was primarily driven not by the older aspen trees, but by a young, dense understory of conifers. Although not considered the dominant vegetation, these conifers provided the density and height requirements of quality grouse habitat. In general, aspen types are most commonly replaced in succession by species such as red maple, sugar maple, white pine, or forest openings, which are not conducive to ruffed grouse production and survival (Hammill and Visser 1984). In this case, however, the course of succession has not substantially decreased the value of the habitat.

Medium aged aspen had a mean HSI value of 0.524 in the open site. It was expected that this habitat type would have a high (or the highest) value of all the types, due to its documented value as a food and cover source for ruffed grouse (Gullion 1970). Lowland conifers had the highest value as grouse habitat according to the model (Table 8),with a mean HSI of 0.533. The middle age-class of aspen had a slightly lower mean HSI value, but it contributed more (0.081) to the overall HSI than the lowland conifer type (0.078) because of its higher percentage of total area. Hardwoods had the lowest mean value, 0.055.

Table 8. Overall HSI values for the PRCSF open and closed sites. Weighted HSI is the mean HSI for the habitat type * the percent of area in that habitat type.

Habitat type	Open site		Closed site	
	Mean HSI	Weighted HSI	Mean HSI	Weighted HSI
Aspen 1-10 yr.	.187	.018	.165	.013
Aspen 11-29 yr.	.524[a]	.081	.345	.035
Aspen 30+ yr.	.495[b]	.043	.161	.011
Upland hardwoods	.055	.013	.032	.006
Lowland hardwoods	.123	.010	.400	.018
Pine 1-30 yr.	.117	.000	.414	.014
Pine 31+ yr.	.189	.022	.206	.043
Lowland conifers	.533	.078	.348	.061
Jack pine	.269	.004	.247	.014
Other	.000	.000	.000	.000
Overall HSI		.27		.21

[a]Mean HSI for aspen 11-29 years in the open site is significantly different from mean HSI for aspen 11-29 years in the closed site (Student's t-test, $p < .10$).
[b]Mean HSI for aspen 30 + years in the open site is significantly different from mean HSI for aspen 30 + years in the closed site (Student's t-test, $p < .01$).

In the closed site, aspen 30 years and older had a lower mean HSI value than the open site, 0.161. As in the open site, young conifers were present in this habitat type, but the understory did not provide density and height requirements of the model (Appendix I, Figure 1 and 3). Medium aged aspen in the closed site also had a lower mean HSI value than in the open site, 0.345. Young pine had the highest HSI value of all the habitat types in the closed site (0.414), but made up the lowest percentage of total area. The weighted HSI value for lowland conifers had the highest numerical effect (0.061) on the overall HSI for the closed site. This effect comes from the high percentage of total area, multiplied by a fairly high mean HSI value of 0.348.

Overall, the open site had a weighted HSI value of 0.27, which was slightly higher than the overall value for the closed site (0.21). Values were generally lower than expected. Only 2 stands in each site had a perfect HSI score of 1.0. Both perfect scores in the open site were in aspen > 30 years, owing to the large number of young conifers in those stands. In the closed site, both perfect scores were in aspen 11-29 years, a habitat type which was expected to be of high value for grouse. Including those which had perfect scores, 9 stands in the open site and 8 stands in the closed had HSI scores > 0.9.

Although the HSI scale in the model is only a relative scale, it is generally assumed that a stand with a value over 0.5 would provide at least marginal habitat. Twenty-five stands in the open site (26.6%) and 20 stands in the closed (18.9%) had values of 0.5 or higher. In the open site, 88% of stands with scores over 0.5 were in aspen types. In the closed site, only 40% of stands with scores over 0.5 were in aspen types, and all types except hardwoods had at least one stand with a value over 0.5.

Weighted HSI values were also calculated for the North and South areas of the closed site (Table 9). Although the North and South areas have different vegetation distributions, the overall area quality is numerically similar. The South area had a slightly higher overall HSI score than the North area. Pine over 30 years contributed 0.072 to the overall value of 0.207 in the North area. Young and old age classes of aspen had a very small effect on the overall value, contributing only 0.003 each. Lowland conifers added significantly more, at 0.041. In the South area, lowland conifers contributed 0.076 to the overall value of 0.220. Medium aged aspen added 0.045, and young and old aspen added more than in the North area (0.020 and 0.018).

To investigate the relationship between model variables and HSI values, Pearson correlation coefficients and related P-values were calculated. The interspersion (winter food) variable was not used in this analysis because nearly all stands contained the minimum requirements to receive an index value of 1.0 (Appendix I, Figure 5). Equivalent stem density was significantly correlated with HSI value in 7 of 8 habitat types in the open site ($p < 0.10$) (Table 10). ESD was not correlated with HSI value in the lowland hardwoods type, because all 4 stands in that habitat type had very high stem densities. In young aspen, shrub and deciduous heights were also correlated with HSI value. At 10 years and younger, the number of aspen stems are usually above minimum requirements; the height of stems to provide cover is the limiting factor. Young pine was not included in the analysis because of low sample size.

Table 9. Overall HSI values for the North and South areas of the Pigeon River Country State Forest closed site. Weighted HSI is the mean HSI for the habitat type * the percent of area in that habitat type.

Habitat type	North area Weighted HSI	South area Weighted HSI
Aspen 1-10 yr.	.003	.020
Aspen 11-29 yr.	.023	.045
Aspen 30+ yr.	.003	.018
Upland hardwoods	.007	.006
Lowland hardwoods	.012	.022
Pine 1-30 yr.	.025	.005
Pine 31+ yr.	.072	.020
Lowland conifers	.041	.076
Jack pine	.021	.008
Other	.000	.000
Overall HSI	.207	.220

Table 10. Pearson correlation coefficients (r) and associated probabilities (P) for individual variables versus HSI values in each habitat type in the open site of the PRCSF.

	ESD[a]		SHR. HT.		DEC. HT.		CON. HT.	
Habitat type	r	P	r	P	r	P	r	P
Aspen 1-10 yr.	.49	.033	.57	.027	.78	.0001	-.41	n.s.[b]
Aspen 11-29 yr.	.55	.02	-.01	n.s.	.09	n.s.	-.01	n.s.
Aspen 30 + yr.	.75	.0005	-.21	n.s.	.38	n.s.	-.39	n.s.
Hardwoods	.74	.02	-.45	n.s.	-.51	n.s.	-.88	n.s.
Lowland hardwoods	.07	n.s.	.35	n.s.	.72	n.s.	-[c]	-
Pine 1-30 yr.	-	-	-	-	-	-	-	-
Pine 31 + yr.	.91	.0002	.48	n.s.	.25	n.s.	-.68	.03
Lowland conifers	.99	.004	.88	n.s.	-.59	n.s.	-.99	.001
Jack pine	.93	.003	-.25	n.s.	.32	n.s.	-.63	n.s.

[a]Variable abbreviations are as follows: ESD = equivalent stem density, SHR. HT. = height of deciduous shrubs, DEC. HT. = height of deciduous trees, and CON. HT. = low branch height of conifers.
[b]Not significant (P > 0.10)
[c]Not enough data for analysis

Table 11. Pearson correlation coefficients (r) and associated probabilities (P) for individual variables versus HSI values in each habitat type in the closed site of the PRCSF.

	ESD[a]		SHR. HT.		DEC. HT.		CON. HT.	
Habitat type	r	P	r	P	r	P	r	P
Aspen 1-10 yr.	-.03	n.s.[b]	.95	.0001	.86	.0001	-.07	n.s.
Aspen 11-29 yr.	.79	.0001	.07	n.s.	.33	n.s.	-.19	n.s.
Aspen 30 + yr.	.85	.0001	.06	n.s.	-.05	n.s.	-.18	n.s.
Hardwood	.87	.001	-.55	n.s.	-.24	n.s.	-.69	n.s.
Lowland hardwoods	.87	n.s.	.97	n.s.	-.75	n.s.	-[c]	-
Pine 1-30 yr.	.87	.005	.63	n.s.	.58	n.s.	.07	n.s.
Pine 31 + years	.97	.0001	.70	.04	.26	n.s.	-.44	n.s.
Low conifer	.57	n.s.	.79	.04	-.37	n.s.	-.92	.001
Jack pine	.76	.01	-.05	n.s.	.02	n.s.	-.82	.004

[a]Variable abbreviations are as follows: ESD = equivalent stem density, SHR. HT. = height of deciduous shrubs, DEC. HT. = height of deciduous trees, and CON. HT. = low branch height of conifers.
[b]Not significant (P > 0.10)
[c]Not enough data for analysis

Equivalent stem density was significantly correlated with HSI values in 6 of 9 habitat types in the closed site ($p < 0.10$) (Table 11). Again, ESD was not correlated with HSI in lowland hardwoods. ESD was also not correlated with HSI in aspen 1-10 years or in lowland conifers. In the young aspen type, shrub height and deciduous height were correlated with HSI values ($p < 0.001$).

Because of its weight in the HSI equation, it was expected that the ESD variable would be highly correlated with final HSI value. The Michigan model (Hammill and Moran 1986) suggests an optimum equivalent stem density of 12085 or greater stems per hectare (Appendix I, Figure 1). Below that density, the value of the stand decreases linearly to 0 at about 5000 stems per hectare. Lowland conifers had the highest stem density of all habitat types in both sites (Table 12, Table 13). In the open site, young aspen and lowland conifers had mean equivalent stem densities greater than the optimum of 12085 stems per hectare called for in the Michigan model. In the closed site, young pine, young aspen and lowland hardwoods had mean ESDs greater than the optimum. In both sites, hardwoods have very low mean equivalent stem densities (< 5000 stems/ha). The largest discrepancy in stem densities between the sites was in young pine stands, which were more dense in the closed site (14288 stems/ha) than in the open site (5375 stems/ha).

Because of the weighting process, looking at straight stem densities did not give an accurate representation of how much each variable contributed to the ESD. The percentage that each weighted component contributed to the ESD was calculated for each habitat type to get a better picture of which component was driving the association. In the young aspen type, deciduous stems (including aspen) accounted for 75.9% of the mean

Table 12. Mean deciduous, conifer and shrub stems/ha (SE), and equivalent stem density for each habitat type sampled in the open site of the PRCSF.

Habitat type	Deciduous Stems/ha		Conifer Stems/ha		Shrub Stems/ha		Equivalent stem density	
Aspen 1-10 yr.	9585	(1212)	498	(171)	2102	(587)	12629	(1616)
Aspen 11-29 yr.	3981	(499)	1519	(317)	2062	(1036)	11086	(1614)
Aspen 30+ yr.	2570	(366)	2154	(490)	939	(367)	11656	(1826)
Upland hardwoods	4033	(721)	25	(21)	162	(65)	4214	(780)
Lowland hardwoods	2667	(1085)	333	(333)	19067	(10919)	13533	(4345)
Pine 1-30 yr.	1767	(1500)	900	(233)	17	(17)	5375	(2442)
Pine 31+ yr.	1177	(295)	1404	(220)	805	(468)	7196	(738)
Lowland conifers	992	(147)	7242	(2548)	2350	(2162)	31133	(10628)
Jack pine	2681	(944)	1443	(313)	124	(31)	8514	(1219)

Table 13. Mean deciduous, conifer and shrub stems/ha (SE), and equivalent stem density for each habitat type sampled in the closed site of the PRCSF.

Habitat type	Deciduous Stems/ha		Conifer Stems/ha		Shrub Stems/ha		Equivalent stem density	
Aspen 1-10 yr.	10146	(1216)	400	(86)	2958	(1006)	13225	(1449)
Aspen 11-29 yr.	4535	(446)	952	(167)	995	(206)	8841	(630)
Aspen 30+ yr.	1938	(237)	1680	(852)	774	(345)	9045	(3372)
Upland hardwoods	2579	(321)	164	(71)	200	(83)	3335	(542)
Lowland hardwoods	1617	(409)	500	(362)	20167	(12053)	13700	(5607)
Pine 1-30 yr.	1138	(554)	3233	(801)	433	(119)	14288	(3609)
Pine 31+ yr.	1222	(319)	1384	(257)	247	(84)	6882	(1158)
Lowland conifers	721	(172)	3413	(518)	4308	(1056)	16525	(2153)
Jack pine	1290	(819)	2493	(638)	207	(107)	11367	(2460)

ESD in the open site (Table 14), and 76.7% in the closed (Table 15). In aspen 11-29 years of age, conifers stems (weighted) began to contribute a significant amount to the mean Equivalent Stem Density. In the open site, 54.8% of the mean ESD in middle age aspen stands were conifer stems, while deciduous stems accounted for only 35.9%. Conifer stems made up 43.1% of the mean ESD of middle age aspen in the closed site. By the 30+ age class, conifers provided about 74% of the ESD in both sites. Shrub stems only contribute substantial numbers to the ESD in one habitat type, lowland hardwoods.

To assess the relationship of stem densities to HSI values even further, correlation coefficients and associated probabilities were calculated for separate unweighted components of the equivalent stem density (Table 16, Table 17). Components tested were stem densities of: aspen of all size classes and other deciduous trees combined; other deciduous trees; aspen of all size classes; aspen < 9 cm dbh (A1); aspen 9 - 18 cm dbh (A2); aspen > 18 cm dbh (A3); conifers of all size classes; and shrubs.

In the open site, densities of conifer stems were correlated with HSI values in all habitat types tested except lowland hardwoods ($p < 0.10$) (Table 16). The correlation in the young aspen type between HSI and the density of large aspen stems is probably an artifact caused by the low frequency of large aspen stems. Correlations associated with medium and total aspen stems within the hardwood habitat type are also artifacts caused by low frequency.

In the closed site, densities of conifer stems were correlated with HSI values in all habitat types tested except lowland hardwoods and lowland conifers (Table 17). In young aspen, densities of deciduous stems, total aspen stems, and small and medium aspen stems

Table 14. Percent of mean equivalent stem density for deciduous, conifer and shrub stems for each habitat type sampled in the open site of the PRCSF.

Habitat type	% of ESD Deciduous	% of ESD Conifer	% of ESD Shrub
Aspen 1-10 yr.	75.9	15.8	8.3
Aspen 11-29 yr.	35.9	54.8	9.3
Aspen 30+ yr.	22.0	73.9	4.0
Upland hardwoods	95.7	2.4	1.9
Lowland hardwoods	19.7	9.8	70.4
Pine 1-30 yr.	32.9	67.0	0.0
Pine 31+ yr.	16.4	78.0	5.6
Lowland conifers	3.2	93.0	3.8
Jack pine	31.5	67.8	0.7

Table 15. Percent of mean equivalent stem density for deciduous, conifer and shrub stems for each habitat type sampled in the closed site of the PRCSF.

Habitat type	% of ESD Deciduous	% of ESD Conifer	% of ESD Shrub
Aspen 1-10 yr.	76.7	21.1	11.2
Aspen 11-29 yr.	51.3	43.1	5.6
Aspen 30+ yr.	21.4	74.3	4.3
Upland hardwoods	77.3	19.7	3.0
Lowland hardwoods	11.8	14.6	73.6
Pine 1-30 yr.	8.0	90.5	1.5
Pine 31+ yr.	17.8	80.4	1.8
Lowland conifers	4.4	82.6	13
Jack pine	11.3	87.7	.9

Table 16. Pearson correlation coefficients (r) and associated probabilities (P) for separate stem density components of the Equivalent Stem Density versus HSI values in each habitat type in the open site of the PRCSF.

	Deciduous/ Aspen		Deciduous		Aspen		A1[a]		A2		A3		Conifer		Shrub	
Habitat type	r	P	r	P	r	P	r	P	r	P	r	P	r	P	r	P
Aspen 1-10 yr.	.24	n.s.[b]	.20	n.s.	-.06	n.s.	-.46	n.s.	-.08	n.s.	1	.0001	.75	.0002	-.04	n.s.
Aspen 11-29 yr.	.14	n.s.	.03	n.s.	.07	n.s.	.01	n.s.	.26	n.s.	-.23	n.s.	.58	.009	.16	n.s.
Aspen 30+ yr.	-.12	n.s.	-.11	n.s.	.02	n.s.	.10	n.s.	-.14	n.s.	-.17	n.s.	.70	.002	.15	n.s.
Hardwoods	.66	.05	.64	.05	.94	.001	.94	.001	-	-	-	-	.95	.0001	.56	n.s.
Lowland hardwoods	-.84	n.s.	-.81	n.s.	-.99	.005	-.99	.005	-	-	-	-	.24	n.s.	.17	n.s.
Pine 1-29 yr.	-[c]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pine 30+ yr.	.27	n.s.	-.04	n.s.	.43	n.s.	.40	n.s.	-.04	n.s.	.08	n.s.	.75	.01	-.26	n.s.
Lowland conifers	-.51	n.s.	-.49	n.s.	-.27	n.s.	-.73	n.s.	-	-	.42	n.s.	.99	.0002	.44	n.s.
Jack pine	.22	n.s.	.05	n.s.	.27	n.s.	.29	n.s.	-.43	n.s.	.11	n.s.	.74	.06	-.05	n.s.

[a]Size class abbreviations are as follows: A1 = aspen < 9 cm dbh, A2 = aspen 9 - 18 cm dbh, A3 = aspen > 18 cm dbh
[b]Not significant (P > 0.10)
[c]Not enough data for analysis

Table 17. Pearson correlation coefficients (r) and associated probabilities (P) for separate stem density components of the Equivalent Stem Density versus HSI values in each habitat type in the closed site of the PRCSF.

	Deciduous/ Aspen		Deciduous		Aspen		A1[a]		A2		A3		Conifer		Shrub	
Habitat type	r	P	r	P	r	P	r	P	r	P	r	P	r	P	r	P
Aspen 1-10 yr.	-.25	n.s.[a]	.68	.003	-.44	.09	-.47	.07	.82	.0001	-	-	.74	.001	-.00	n.s.
Aspen 11-29 yr.	.04	n.s.	.02	n.s.	-.05	n.s.	-.11	n.s.	.23	n.s.	.02	n.s.	.76	.0001	.13	n.s.
Aspen 30+ yr.	-.30	n.s.	-.31	n.s.	-.17	n.s.	-.08	n.s.	-.28	n.s.	.26	n.s.	.87	.0001	.02	n.s.
Hardwoods	.58	.08	.51	n.s.	.60	.07	.60	.06	-	-	-.17	n.s.	.89	.0006	.73	.02
Lowland hardwoods	-.30	n.s.	-.30	n.s.	-[b]	-	-	-	-	-	-	-	.40	n.s.	.74	n.s.
Pine 1-29 yr.	.36	n.s.	.41	n.s.	-.09	n.s.	-.09	n.s.	-	-	-	-	.90	.002	.72	n.s.
Pine 30+ yr.	.55	.10	.61	.06	.17	n.s.	-.18	n.s.	-.03	n.s.	-.28	n.s.	.93	.0001	-.44	n.s.
Lowland conifers	.58	n.s.	.62	n.s.	-.26	n.s.	.02	n.s.	-.06	n.s.	-.47	n.s.	.40	n.s.	.54	n.s.
Jack pine	-.20	n.s.	-.26	n.s.	.46	n.s.	.55	n.s.	.07	n.s.	-.25	n.s.	.80	.006	.00	n.s.

[a]Size class abbreviations are as follows: A1 = aspen < 9 cm dbh, A2 = aspen 9 - 18 cm dbh, A3 = aspen > 18 cm dbh
[b]Not significant (P > 0.10)
[c]Not enough data for analysis

were correlated with HSI values. In pine 30+ years, combined deciduous and aspen stems and deciduous stems were correlated with HSI values. A correlation exists between deciduous stems with HSI values in the hardwood type, but correlations of aspen stems within that type are probably due to the low frequency of those stems.

Because of its historical importance as grouse habitat, aspen stands were further analyzed for stem densities by age. Gullion (1970) provided a range of stem densities which had significant use by ruffed grouse. He suggested that ruffed grouse make little use of regenerating aspen until the sapling density has thinned to about 19700 stems per hectare, and that heavy use continues until stem density reaches about 7400 stems per hectare. Only a few aspen stands under 10 years of age in the open and closed sites had the optimum value (or greater) in aspen stems alone (Figure 2, Figure 3). When other species are added to make the equivalent stem density, substantially more stands reach the optimum. Notice that although the density of aspen stems across ages is consistent between the open and closed site, ESDs are higher in the open site at ages 10 - 60 years.

It has been argued whether or not conifers contribute to cover for ruffed grouse or provide cover for predators. Young balsam fir in the understory of mature aspen forests has been shown to provide cover for drumming grouse in Wisconsin (Kubisiak et al. 1980), and conifers are considered important winter cover for ruffed grouse in New York State (Bump et al. 1947, Edminster 1947). Yet in the original ruffed grouse model (Cade and Sousa 1985), on which the Michigan model is based, it is suggested that the presence of any conifers in an otherwise suitable habitat will reduce suitability of fall to spring cover by offering concealment for predators. In that model, there is a penalty assigned to the

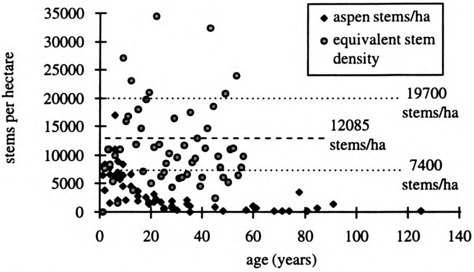


Figure 2. Aspen stems per hectare and equivalent stem density in various aged aspen stands in the open site of the PRCSF. Dashed lines indicate maximum (19700) and minimum (7400) stems/ha called for by Gullion (1970), and optimum (12085) stems/ha in the Michigan model (Hammill and Moran 1986).

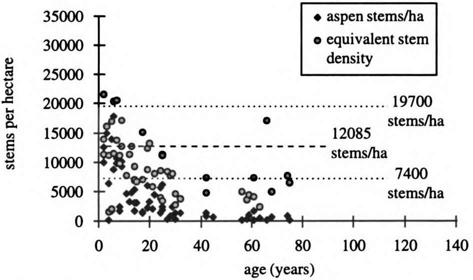


Figure 3. Aspen stems per hectare and equivalent stem density in various aged aspen stands in the closed site of the PRCSF. Dashed lines indicate maximum (19700) and minimum (7400) stems/ha called for by Gullion (1970), and optimum (12085) stems/ha in the Michigan model (Hammill and Moran 1986).

HSI value which corresponds to the percentage of conifers in the stand being assessed.

The Michigan model alters this thinking dramatically, and assumes that a conifer provides valuable cover for ruffed grouse; according to the weighting procedure, 4 times more valuable than a deciduous tree. If conifers do indeed provide valuable cover, the important role that they play as grouse cover in the PRCSF cannot be ignored. In most habitat types in the study area, HSI scores are correlated with conifer density, and without them, stem densities would not reach near optimum levels. Contrary to the customary view of young, regenerating aspen stands, most aspen stands in the study between the ages of 11 - 29 would be of negligible value without the contribution of conifer stems. This may be a trend of northern Michigan forests, or unique to the circumstances at the PRCSF.

Movements

In 1993, there were 15 birds in the open site and 19 birds in the closed site that were located during at least 5 different weeks. Four birds in the open site and 5 birds in the closed site fit the into the category of Type I non-dispersers (Table 18). Type I non-dispersers had a mean home range of 44.3 ha in the open site, and 49.7 ha in the closed site in 1993 (home ranges included were calculated using the convex polygon method; harmonic mean home ranges showed similar trends). Although the closed site had a slightly higher mean, there was no significant difference in home range sizes between sites.

Type I males in the closed site had a significantly larger mean home range (72.7 ha) than males in the open site (42.7 ha) ($p < 0.10$). Closed site males also had a significantly larger mean home range than closed site females (34.5 ha) ($p < 0.10$). No other significant differences were detected between sites or between sex or age classes. Because of low sample sizes, age categories were not split by sex.

Four birds in the open and 8 in the closed site were categorized as Type II non-dispersers (Table 18). Type II birds had a mean home range of 148.7 ha in the open site, and a mean home range of 163.9 ha in the closed site in 1993 (Table 18). In both sites, Type II juvenile birds had a larger mean home ranges than Type II adults (not significantly different). There were no significant differences in mean home range between sites or between categories ($p > 0.10$).

In 1993, there were 7 dispersers in the open site (Table 19). Those birds had a mean net dispersal distance of 940 m. Adults moved significantly farther than juveniles ($p < 0.10$). The 6 dispersers in the closed site in 1993 moved slightly farther (1068 m)

Table 18. Mean home range size (ha) for Type I and Type II non-dispersers in the PRCSF open and closed sites, 1993.

		Open site			Closed site		
		$\overline{X}$ (SE)		N	$\overline{X}$ (SE)		N
Type I	Total	44.3	(5.0)	4	49.7	(10.0)	5
	Male	42.7	(6.8)A[a]	3	72.7	(3.9)Ba	2
	Female	48.9	-	1	34.5	(5.8)b	3
	Sex unk.	-	-	0	-	-	0
	Adult	44.3	(5.0)	4	54.4	(11.3)	4
	Juvenile	-	-	0	30.8	-	1
	Age unk.	-	-	0	-	-	0
Type II	Total	148.7	(21.0)	4	163.9	(24.5)	8
	Male	177.1	-	1	144.5	(17.3)	7
	Female	139.2	(26.5)	3	299.6	-	1
	Sex unk.	-	-	0	-	-	0
	Adult	135.2	(41.9)	2	131.3	(19.9)	5
	Juvenile	162.1	(23.0)	2	218.1	(43.8)	3
	Age unk.	-	-	0	-	-	0

[a] Capital letters indicate significant difference between sites (Student's t-test, $p < 0.10$). Small letters indicate significant difference between sex or age categories (Student's t-test, $p < 0.10$).

Table 19. Mean dispersal distance (m) for ruffed grouse in the PRCSF open and closed sites, 1993.

	Open site			Closed site		
	$\overline{X}$(SE)		N	$\overline{X}$(SE)		N
Total	939.5	(103.6)	7	1068.2	(271.2)	6
Male	1058.5	(59.0)	3	730.3	(167.8)	2
Female	850.2	(172.2)	4	1237.2	(388.1)	4
Sex unk.	-	-	0	-	-	0
Adult	1064.3	(91.3)a[a]	5	963.5	(360.3)	4
Juvenile	627.4	(76.5)b	2	1277.7	(508.7)	2
Age unk.	-	-	0	-	-	0

[a]Small letters indicate significant difference between sex or age categories (Student's t-test, $p < 0.10$).

than those in the open site, but the difference was not significant ($p > 0.10$). Juvenile birds in the closed site moved a mean distance of 1278 m while juveniles in the open site moved only 627 m, but again the difference was not significant.

In 1994, 28 birds were analyzed for movement patterns in the open site, and 26 in the closed. There were 4 birds in the open site and 4 in the closed site which fit the description of Type I non-dispersers (Table 20). All 4 in the closed site and 3 in the open were male birds. Similar to the 1993 data, Type I birds had a mean home range size of 45.5 ha in the open site and 39.4 ha in the closed site. Sex and age classes could not be compared due to low sample sizes.

There were 9 Type II birds in the open site in 1994 with a mean home range of 106.7 ha (Table 20). Eleven Type II birds in the closed site had a mean home range of 105.1 ha. These values were lower than those for 1993. Closed site males had a significantly smaller mean home range size (63.6 ha) than closed site females (114.3 ha) and open site males (101.5 ha) ($p < 0.10$). No other significant differences were detected.

Unlike 1993 dispersers, the 15 dispersers in the open site in 1994 moved farther (1784 m) than those in the closed site (1132 m) (Table 21). Females in the open site moved significantly farther than females in the closed site ($p < 0.10$). In the closed site, males moved a significantly higher net distance (1692 m) than females (651 m) ($p < 0.10$). Juveniles in the open site in 1994 moved a farther mean net distance (2275 m) than any other sex or age category in either year.

In the closed site in 1994, 4 birds exhibited dispersal movements after week 16 (November-December). These birds were not considered dispersers. Small and Rusch

Table 20. Mean home range size (ha) for Type I and Type II non-dispersers in the PRCSF open and closed sites, 1994.

		Open site			Closed site		
		X̄	(SE)	N	X̄	(SE)	N
Type I	Total	45.5	(9.4)	4	39.4	(8.3)	4
	Male	37.8	(7.4)	3	39.4	(8.3)	4
	Female	-	-	0	-	-	0
	Sex unk.	68.9	-	1	-	-	0
	Adult	25.4	-	1	39.4	(8.3)	4
	Juvenile	52.3	(9.3)	3	-	-	0
	Age unk.	-	-	0	-	-	0
Type II	Total	106.7	(16.7)	9	105.1	(16.2)	11
	Male	101.5	(14.1)A[a]	4	63.6	(6.5) Ba	2
	Female	111.6	(38.1)	4	114.3	(18.4)b	9
	Sex unk.	108.4	-	1	-	-	0
	Adult	86.4	(11.7)	6	92.3	(20.3)	6
	Juvenile	147.4	(37.5)	3	91.9	(22.2)	3
	Age unk.	-	-	0	163.2	(51.2)	2

[a] Capital letters indicate significant difference between sites (Student's t-test, $p < 0.10$). Small letters indicate significant difference between sex or age categories (Student's t-test, $p < 0.10$).

Table 21. Mean dispersal distance (m) for ruffed grouse in the PRCSF open and closed sites, 1994.

	Open site			Closed site		
	X̄	(SE)	N	X̄	(SE)	N
Total	1784.3	(366.3)	15	1132.0	(222.1)	11
Male	1660.6	(524.4)	7	1692.4	(413.2)a	4
Female	2039.7	(601.7)A[a]	7	650.6	(102.3)Bb	6
Sex unk.	861.7	-	1	1778.8	-	1
Adult	1538.3	(403.2)	9	1109.9	(347.9)	6
Juvenile	2275.4	(856.0)	5	959.1	(288.2)	4
Age unk.	861.7	-	1	1955.8	-	1

[a]Capital letters indicate siginifcant difference between sites (Student's t-test, $p < 0.10$). Small letters indicate significant difference between sex or age categories (Student's t-test, $p < 0.10$).

(1989) also noted minor dispersal movements in December and January, and considered them shifts in winter range. These shifts may be related to the quality of winter habitat, density dependent factors, or some combination of the two. No birds in 1993 or in the open site in 1994 exhibited such movements.

Birds in the closed site were split between the North and South areas in 1993 and 1994 (Table 22, Table 23). In 1993, there was only 1 bird in each dispersal type in the North area, so no statistical comparisons could be made. However, home ranges of Type I and II birds, and distance of dispersal were all larger than the means for the South area birds. In 1994, home ranges and dispersal distances were also consistently larger, but no statistically significant differences were detected ($p > 0.10$).

Overall, there were no noticeable trends in site, sex or age classes that were consistent between years. In a similar telemetry study, Small and Rusch (1989) measured a mean net movement of 4.82 km for juvenile females over several years of study. Collared juvenile males moved only half of that distance, 2.14 km. In this study in 1993, no birds in either site moved over 4 km. In 1994, a juvenile female in the open site moved nearly 5 km. Few birds in 1994 and none in 1993 approached these distances, and means were considerably less. Small and Rusch (1989), however, used only birds which were captured before September 10, to ensure that birds would be monitored for the duration of fall dispersal. In this study, it was necessary to include birds which were caught as late as early October.

Godfrey and Marshall (1969) also showed that juvenile female ruffed grouse move farther than males in autumn. A compilation of research results from banding studies

Table 22. Mean home range size (ha) for Type I and Type II birds and dispersal distances (m) for Type III birds in the North and South areas of the closed site of the PRCSF, 1993.

	North area		South area	
	$\overline{X}$ (SE)	N	$\overline{X}$ (SE)	N
Type I	68.6 -	1	45.0 (11.3)	4
Type II	205.1 -	1	158.0 (27.4)	7
Type III	1997.9 -	1	882.3 (241.8)	5

Table 23. Mean home range size (ha) for Type I and Type II birds and dispersal distances (m) for Type III birds in the North and South areas of the closed site of the PRCSF, 1994.

	North area		South area	
	$\overline{X}$ (SE)	N	$\overline{X}$ (SE)	N
Type I	50.3 (11.0)	2	28.6 (8.0)	2
Type II	121.5 (16.3)	5	91.4 (26.5)	6
Type III	1167.3 (334.2)	7	1070.2 (243.6)	4

provided in Bergerud and Gratson (1988) indicated that juveniles generally move farther than adults and females moved farther than males, and that juveniles and females have correspondingly larger home ranges. Although these trends were observed in some cases in this study, few significant differences were detected. Additionally, it was expected for birds in the site open to hunting to move farther and have larger home ranges in the fall due to increased flushes by hunters. Fall movements, however, may be more related to the quality of habitat present or density dependent factors. Low sample sizes may have contributed to results which were not consistent between years. Combination of the data across years was avoided at this point in the study, so that factors which may be associated with yearly fluctuations of the population could be assessed.

Habitat use

In the open site in 1993, 16 birds were located on at least 10 separate days (Table 24). There were 767 locations taken on those birds, with a mean of 48 locations per bird. On this site, 22.2 % of all grouse locations were in aspen between 11 and 29 years of age, and 20.2 % were in aspen between 1 and 10 years of age. In total, 56.8% of locations were in aspen of any age class. Pine 1-29 years of age and jack pine types were used very infrequently, 0.2% of all locations each.

In the closed site in 1993, all but 3 birds were captured and stayed within the South area. The 3 birds in the North area had a total of 135 locations, for a mean of 45 locations per bird. Pine over 30 years of age was used heavily, with 32.6% of all locations that type. Aspen of all age classes comprised 36.4% of the total number of locations. Jack pine was used frequently also, with 27% of locations being in that type.

In the South area, 16 birds had a total of 741 locations, for a mean of 46 locations per bird. More than half (56.2%) of all locations were in aspen of any age class. Pine > 30 years and hardwoods were used moderately (8-11%), while young pine and jack pine were used rarely.

There were fewer locations per bird in 1994, due to reduced personnel and a larger number of birds to locate. The open site had a sample size of 30 birds, with 850 daily locations, with a mean of 28 locations per bird. As in 1993, a high percentage of locations were in medium aged aspen (25.8%). More than half (53.8%) of locations were in aspen types.

Table 24. Number and percent of grouse locations in each habitat type by site and year.

Habitat type	Open 1993		Open 1994		Closed 1993				Closed 1994			
					North		South		North		South	
	N	%	N	%	N	%	N	%	N	%	N	%
Aspen 1-10 yr.	155	20.2	107	12.6	17.5	13.0	112.5	15.2	28.5	6.2	80.5	23.3
Aspen 11-29 yr.	170	22.2	219	25.8	14	10.4	180.5	24.4	25.5	5.6	34	9.8
Aspen 30 + yr.	110.5	14.4	130.5	15.4	17.5	13.0	123	16.6	15.5	3.4	40	11.6
Hardwoods	90	11.7	105	12.4	2.5	1.9	63	8.5	4	0.9	77	22.3
Lowland hardwoods	39.5	5.1	76.5	9.0	0	0.0	57.5	7.8	2.5	0.5	21.5	6.2
Pine 1-29 yr.	1.5	0.2	14	1.6	1.5	1.1	9.5	1.3	42.5	9.3	1	0.3
Pine 30 + yr.	90.5	11.8	42	4.9	44	32.6	84	11.3	271	59.3	30.5	8.8
Lowland conifers	71.5	9.3	133.5	15.7	1.5	1.1	50	6.8	14	3.1	32	9.2
Jack pine	1.5	0.2	1.5	0.2	36.5	27.0	13.5	1.8	39.5	8.6	12	3.5
Other	37	4.9	21	2.5	0	0.0	47.5	6.4	14	3.1	17.5	5.1
Total	767		850		135		741		457		346	

In 1994, the North area of the closed site was trapped with more intensity than in 1993, resulting in a higher number of collared birds. The North area had 14 birds eligible to be used in the habitat use analysis with 457 locations, for a mean of 33 locations per bird. Again, the majority of bird locations (59.3%) were in pine 30+ years. Aspen types were used 15.2% of the time, considerably less than in 1993. Differences may be a result of the considerably larger sample size in the 1994 analysis.

The South had 13 birds and 346 locations, with a mean of 27 locations per bird. Aspen 1-10 years was used more frequently in the South area in 1994 than in 1993, with 23.3% of all locations. Hardwoods were also used more in 1994, with 22.3% of all locations in that type. Aspen of combined age classes accounted for 44.7% of all locations.

Percent of locations in each habitat was categorized by dispersal type to explore the possibility that movement may affect habitat selection. In the open site in both years, the only birds that were located in jack pine were dispersers (Table 25). Dispersers also had a lower percentage of locations in medium aged aspen in 1993 (12.3%) and in 1994 (18.2%) than did Type I and II non-dispersers.

In the North area of the closed site in 1993, only 1 bird fell into each category (Table 26). The disperser used considerably more jack pine (58.8%) than Type I and II non-dispersers. In 1994, all types used old pine heavily. Type I birds used more medium aspen, while Type II birds used more jack pine.

In the South area of the closed site in 1993, Type I birds used medium aspen heavily (36.5%) (Table 27). Type II birds used all ages of aspen with comparable

Table 25. Number and percent of grouse locations in each habitat type in the open site by dispersal type and year.

	1993						1994					
	Type 1		Type 2		Dispersers		Type 1		Type 2		Dispersers	
Habitat type	N	%	N	%	N	%	N	%	N	%	N	%
Aspen 1-10 yr.	37.5	18.1	33.5	17.2	84	23.7	14	12.6	42	13.8	45.5	11.1
Aspen 11-29 yr.	67	32.4	56.5	29.0	43.5	12.3	52	45.0	88.5	29.1	74.5	18.2
Aspen 30 + yr.	15	7.2	39.5	20.3	53.5	15.1	16.5	14.3	44	14.4	68	16.6
Hardwoods	21.5	10.4	25.5	13.1	43	12.1	15	13.0	39	12.8	45	11.0
Lowland hardwoods	3.5	1.7	2.5	1.3	29.5	8.3	1	.9	41	13.5	34.5	8.4
Pine 1-29 yr.	0	0	1.5	.8	0	0	.5	.4	1.5	.5	12	2.9
Pine 30 + yr.	44.5	21.5	4	2.1	42	11.8	1.5	1.3	9	3.0	30.5	7.4
Lowland conifers	17	8.2	21	10.8	33	9.3	13.5	11.7	32.5	10.8	85	20.7
Jack pine	0	0	0	0	1.5	.4	0	0	0	0	1.5	.4
Other	1	.5	11	5.6	25	7.0	1	.9	6.5	2.1	13.5	3.3
Total	207		195		355		115		304		410	

Table 26. Number and percent of grouse locations in each habitat type in the North area of the closed site by dispersal type and year.

	1993						1994					
	Type 1		Type 2		Dispersers		Type 1		Type 2		Dispersers	
Habitat type	N	%	N	%	N	%	N	%	N	%	N	%
Aspen 1-10 yr.	6.5	13.8	8	16.7	3	7.5	1	1.7	10	5.2	17.5	8.6
Aspen 11-29 yr.	10.5	22.3	2.5	5.2	1	2.5	8	13.3	3.5	1.8	14	6.9
Aspen 30 + yr.	5.5	11.7	11	22.9	1	2.5	1	1.7	5.5	2.8	9	4.4
Hardwoods	0	0	2.5	5.2	0	0	0	0	2	1.0	2	1.0
Lowland hardwoods	0	0	0	0	0	0	.5	.8	0	0	2	1.0
Pine 1-29 yr.	1.5	3.2	0	0	0	0	7.5	12.5	33	17	2	1.0
Pine 30 + yr.	22	46.8	11	22.9	11	27.5	36	60.0	115.5	59.5	119.5	58.9
Lowland conifers	1	2.1	0	0	.5	1.3	.5	.8	5	2.6	8.5	4.2
Jack pine	0	0	13	27.1	23.5	58.8	5.5	9.2	12.5	6.4	21.5	10.6
Other	0	0	0	0	0	0	0	0	7	3.6	7	3.4
Total	47		48		40		60		194		203	

Table 27. Number and percent of grouse locations in each habitat type in the South area of the closed site by dispersal type and year.

	1993						1994					
	Type 1		Type 2		Dispersers		Type 1		Type 2		Dispersers	
Habitat type	N	%	N	%	N	%	N	%	N	%	N	%
Aspen 1-10 yr.	12.5	8.0	62.5	19.7	37.5	14.0	23.5	45.2	39.5	22.8	15.5	14.8
Aspen 11-29 yr.	57	36.5	63	19.8	60.5	22.7	1	1.9	21	12.1	7	6.7
Aspen 30 + yr.	14.5	9.3	50.5	15.9	58	21.7	11.5	22.1	14	8.1	8.5	8.1
Hardwoods	0	0	31	9.7	32	12.0	8	15.4	22	12.7	47	44.8
Lowland hardwoods	18.5	11.9	21.5	6.8	17.5	6.6	5	9.6	16.5	9.5	0	0
Pine 1-29 yr.	0	0	6	1.9	3.5	1.3	0	0	1	.6	0	0
Pine 30 + yr.	22	14.1	40	12.6	22	8.2	0	0	17	9.8	13.5	12.9
Lowland conifers	16	10.3	18.5	5.8	15.5	5.8	2	3.8	22	12.7	5	4.8
Jack pine	2.5	1.6	7.5	2.4	3.5	1.3	0	0	8	4.6	4	3.8
Other	13	8.3	17.5	5.5	17	6.3	1	1.9	12	6.9	4.5	4.3
Total	156		318		267		52		173		105	

intensity, as did dispersers. In 1994, Type I birds seemed to prefer young aspen, and dispersers spent more time in hardwoods (44%).

The percentages mentioned above are for all birds combined, so they may be reflecting the tendency of certain birds to use 1 habitat type frequently or exclusively. The following preference analysis was based on each individual bird with habitat ranked by usage, thus changing the definition of "use". Availability was considered the entire open site for open site birds, and the North or South area of the closed site for closed site birds. In the closed site, birds which were caught in an area did not cross into the other area.

The analysis of preference is a ranking procedure, which is biased towards infrequently used habitat types with low availability. In the open site in both years, young pine was not used in the analysis of preference, due to its low percentage of total area. In the South area of the closed site in both years, jack pine and young pine were not included in the analysis. There were few locations in these habitat types in either year (Table 24).

In the open site in 1993, aspen > 30 years, "other", young aspen, lowland hardwoods and jack pine were used more frequently than they were available (Figure 4a). Lowland conifers, pine > 30 years, aspen 11 - 29 years, and hardwoods were used less than available. Trends were similar in 1994 (Figure 4b). Old aspen had the highest mean HSI value of those habitats used frequently, but those habitats with the highest mean HSI values of the open site (lowland conifers and aspen 11 - 29 years) were used less than would be expected.

In the closed site in 1993, there were not enough bird locations in the North area to carry out the analysis of preference. In the South area, the "other" category, lowland

a) Open site, 1993.

ASPEN > 30 yr.	OTHER	ASPEN 1 - 10 yr.	LOWLAND HARDWOOD	JACK PINE	LOWLAND CONIFER	ASPEN 11 - 29 yr.	PINE > 30 yr.	HARDWOOD
.495	.000	.187	.123	.269	.533	.524	.189	.055

b) Closed site, South area, 1993.

OTHER	LOWLAND HARDWOOD	PINE > 30 yr.	ASPEN > 30 yr.	ASPEN 11 - 29 yr.	ASPEN 1 - 10 yr.	LOWLAND CONIFER	HARDWOOD
.000	.400	.206	.161	.345	.165	.348	.032

DECREASING RANK →

Figure 4. Fall and winter habitat preference for ruffed grouse in the Pigeon River Country State Forest in 1993 and 1994. Grouse habitat preference was not different (Waller Duncan multiple comparison procedure, $p > 0.10$) between underlined habitats. Mean HSI values for each habitat type in each site are given for reference.

c) Open site, 1994.

ASPEN > 30 yr.	LOWLAND HARDWOOD	JACK PINE	OTHER	ASPEN 1 - 10 yr.	LOWLAND CONIFER	ASPEN 11 - 29 yr.	PINE > 30 yr.	HARDWOOD
.495	.123	.269	.000	.187	.533	.524	.189	.055

d) Closed site, South area, 1994.

OTHER	ASPEN > 30 yr.	LOWLAND HARDWOOD	PINE > 30 yr.	ASPEN 1 - 10 yr.	ASPEN 11 - 29 yr.	HARDWOOD	LOWLAND CONIFER
.000	.161	.400	.206	.165	.345	.032	.348

→ DECREASING RANK

Figure 4. (cont'd)

e) Closed site, North area, 1994.

ASPEN 1 - 10 yr.	ASPEN > 30 yr.	LOWLAND HARDWOOD	OTHER	ASPEN 11 - 29 yr.	PINE > 30 yr.	JACK PINE	PINE < 30 yr.	LOWLAND CONIFER	HARDWOOD
.165	.161	.400	.000	.345	.206	.247	.414	.348	.032

DECREASING RANK →

Figure 4. (cont'd)

hardwoods and pine > 30 years were used more than available (Figure 4c). Lowland conifers and hardwoods were used less than available, and aspen types were used in general proportion to availability. Results were similar in 1994, with the exception of older aspen moving up in rank (Figure 4d).

Young and old aspen were used frequently in the North area of the closed site in 1994 (Figure 4e). These habitat types were rare, and used infrequently, but were not eliminated from analysis due to the perceived value of aspen as ruffed grouse habitat. Lowland hardwoods, "other", medium aged aspen, old pine, jack pine and young pine were used in proportion to their availability, while lowland conifers and hardwoods were avoided. As in the open site, lowland conifers had a relatively high mean HSI value in the closed site (0.348) and was plentiful in the South area, but was used infrequently.

It was expected that hardwood types would be avoided in both sites, due to their low stem densities and corresponding low mean HSI values. High ranking of the "other" category would also not be expected according to the model habitat requirements. In both sites in both years, most bird locations which fell into the category "other" were in grass or upland brush. Although these habitat types would have no value as fall/winter cover according to model guidelines, openings and forest/opening edges may provide other valuable habitat components, and were used more or in proportion to their availability.

To analyze the quality of habitat selected, habitat use values were calculated for each bird by multiplying the percent of locations in each habitat type by the mean HSI value for the corresponding types. Mean habitat use values were calculated for each site in each year (Figure 5). Mean habitat use values were not significantly different between the North and South areas of the closed site in 1993 or 1994 ($p > 0.10$). Values were significantly different between the open site (0.311) and the North (0.222) and South areas (0.232) of the closed site in 1993 ($p < 0.10$). Habitat use values were also different between the open site (0.349) and the North (0.226) and South areas (0.204) of the closed site in 1994 ($p < 0.10$). The values for the open site in 1993 and 1994 were slightly higher than the overall HSI value of 0.27, but closed site values were comparable or below overall HSIs.

A common explanation for the fall dispersal of grouse is that birds move to places where their survival is enhanced by a more plentiful food supply or cover from predators. It follows that birds would have to pass through marginal or poor quality habitat to reach a satisfactory destination. To explore this possibility, mean habitat use values were calculated for each dispersal type by site and year (Figure 6 - Figure 10). The North area in 1993 was not included in this analysis, because each dispersal category consisted of only 1 bird.

In both sites in both years, habitat use values were lower for Type III birds than for Type I birds, but no significant differences were detected between dispersal types between years. The highest habitat use value was for Type I birds in 1994 (Figure 7). The lowest values occurred in the South area of the closed in 1994, because of the use of hardwoods. Even though it was used less frequently than available, there were enough bird locations in the hardwood type to adversely affect habitat use values.

It was assumed that in both sites, birds would use aspen types (and other habitat types with high HSI values) in a higher frequency than their availability. Although that

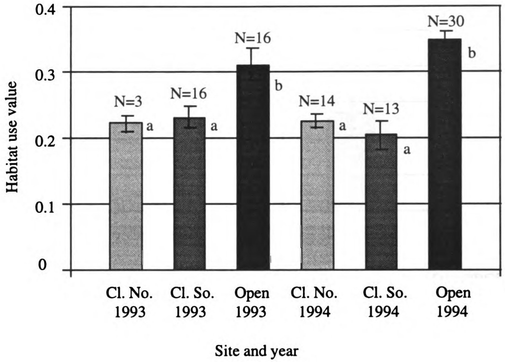


Figure 5. Mean habitat use values by site and year. Error bars are one standard error above and below the mean. Different letters indicate significant difference among habitat use values (Kruskal-Wallis one-way ANOVA, Multiple Comparisons, $p < 0.10$).

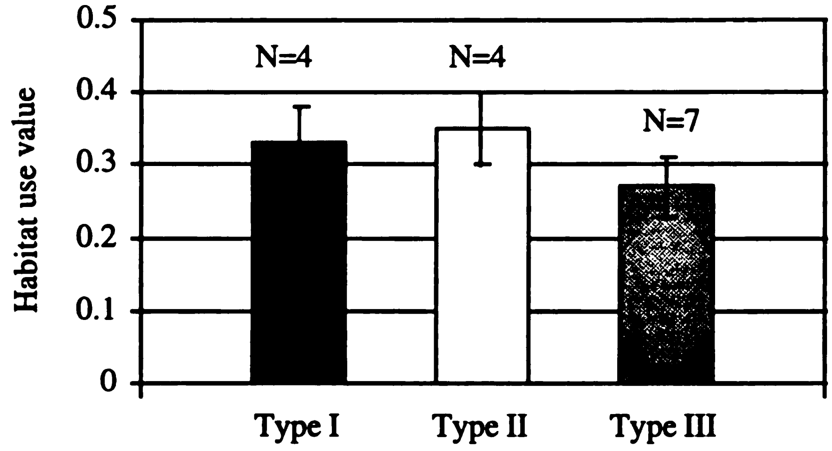


Figure 6. Mean habitat use values by dispersal type in the open site of the PRCSF in 1993. Error bars are one standard error above and below the mean. No significant differences were detected (Kruskal-Wallis one-way ANOVA, $p > 0.10$).

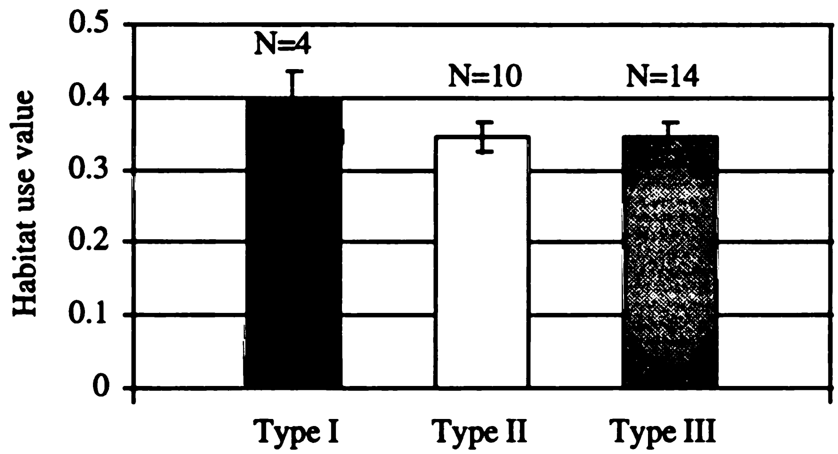


Figure 7. Mean habitat use values by dispersal type in the open site of the PRCSF in 1994. Error bars are one standard error above and below the mean. No significant differences were detected (Kruskal-Wallis one-way ANOVA, $p > 0.10$).

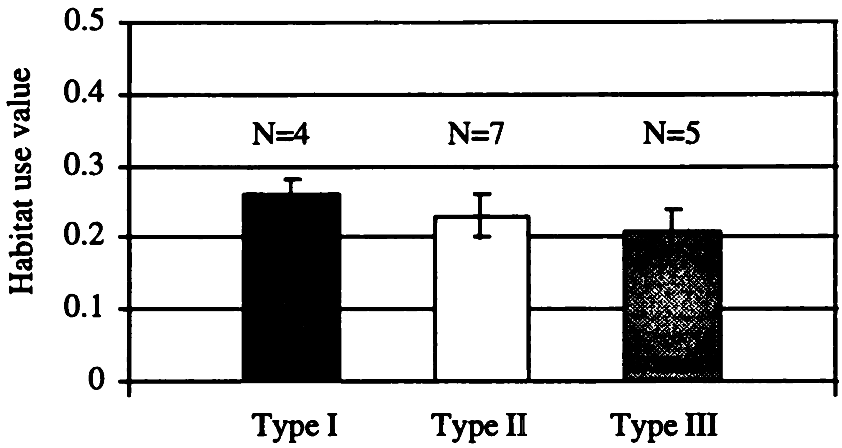


Figure 8. Mean habitat use values by dispersal type in the South area of the closed site of the PRCSF in 1993. Error bars are one standard error above and below the mean. No significant differences were detected (Kruskal-Wallis one-way ANOVA, $p > 0.10$).

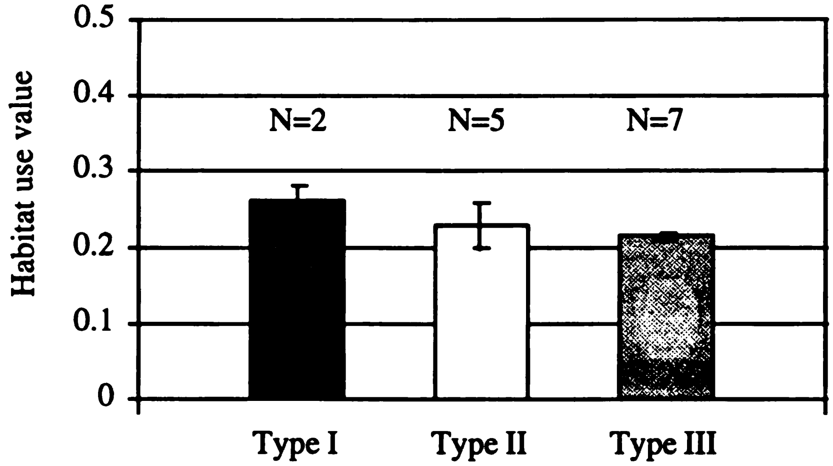


Figure 9. Mean habitat use values by dispersal type in the North area of the closed site of the PRCSF in 1994. Error bars are one standard error above and below the mean. No significant differences were detected (Kruskal-Wallis one-way ANOVA, p > 0.10).

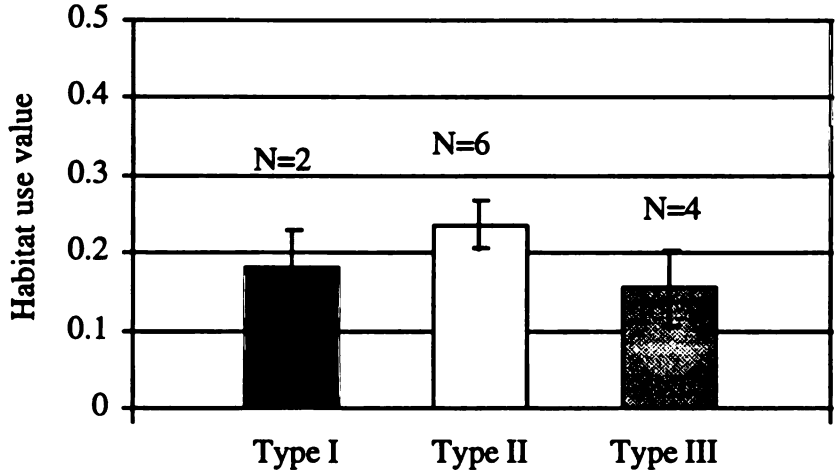


Figure 10. Mean habitat use values by dispersal type in the South area of the closed site of the PRCSF in 1994. Error bars are one standard error above and below the mean. No significant differences were detected (Kruskal-Wallis one-way ANOVA, p > 0.10).

was true in some cases, grouse also frequently made use of habitats which had low values for cover and food requirements according to the model. For example, the "high-tree" pine forest is generally considered low security habitat, where young grouse cannot survive. The only postulated reason for birds using such habitats is that they are unable to compete successfully for more secure habitats in the fall. Such habitats supposedly fail to provide the quality of cover necessary to allow them to live to breeding age (Gullion 1970). The quality of old pine in the closed site was low, and birds were expected to avoid it. Although it was not used significantly more than available, birds in the North area of the closed site did not seem to avoid the highly available older pine types in favor of types with better HSI values.

One weakness in using the Michigan model is that it evaluates the forest on a stand by stand basis, with little regard for the interspersion of habitat types across the landscape. Many researchers have stated that optimal habitat for ruffed grouse is provided by the interspersion of several forest age classes (Cade and Sousa 1985). This model may be improved considerably by including weighting procedures for size of the stand and adjoining habitat edges, an idea which has been explored by Roloff (1994). Although it is beyond the scope of this study, the study sites are in the process of being digitized, at which time landscape variables could be added to the model with relative ease.

Survival

Survival was analyzed from August 4, 1993 and 1994 through May 15 of the following year. Past May 15, the number of censored birds increased to a point where the accuracy of survival analysis would be compromised. In the open site in 1993, 31 birds were used for analysis of survival. Birds which died or were censored within 5 days of capture were not used. Excluded birds included 2 that died of stress or suffocation, 1 that was killed by a mammalian predator, 1 that was censored, and 1 bird whose radio was removed due to retrapping injuries. Two birds that died of stress or suffocation survived past 5 days after capture, and were treated as censored for survival analysis. The overall survival probability in the open site in 1993 was 0.19 (Figure 11).

In the closed site in 1993, 24 birds were used in the survival analysis. Three birds died of stress and 1 was killed by a mammalian predator within 5 days of capture. The overall survival probability in the closed site in 1993 was 0.63 (Figure 11). In 1993, survival probability was significantly higher in the closed site than the open site (Log- rank test, $p < 0.01$). Because there were only 3 birds collared in the North area of the closed site in 1993, a separate survival probability could not be calculated. The South area of the closed site had a survival probability of 0.58 (Figure 12).

In the open site, 1 bird from 1993 survived long enough to be included in the survival analysis for 1994. It was recaptured and recollared, and is included in the total number of collared birds. Of the 47 birds which were collared, 4 that died of stress or suffocation, 1 that was censored, and 1 whose radio was removed within 5 days of capture were eliminated from survival analysis. This resulted in a total of 41 birds to be used in the survival analysis. Overall survival was 0.29 (Figure 13), slightly higher than

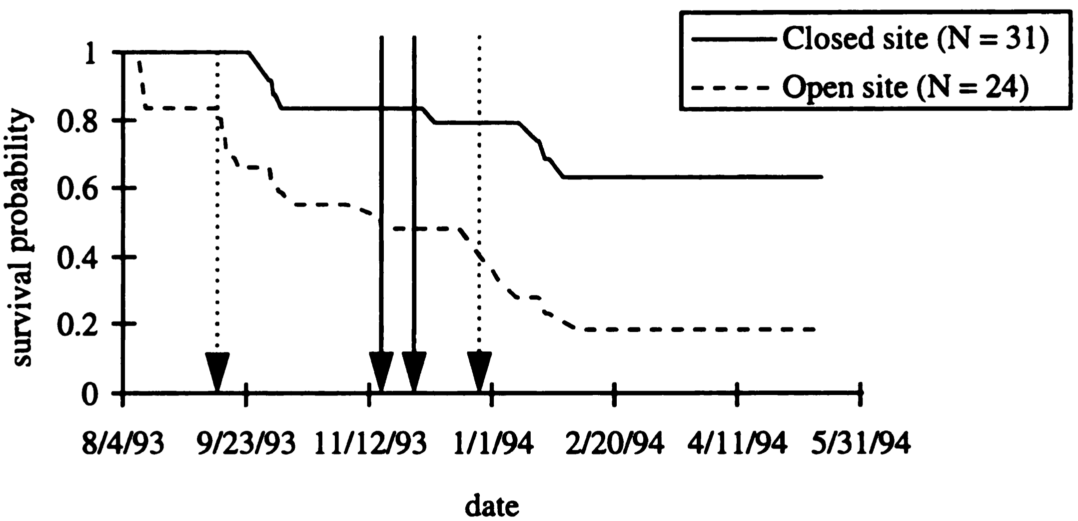


Figure 11. Survival probability for ruffed grouse radio-collared in the PRCSF in 1993. Arrows approximate hunting season, September 15 through December 31, with a 2 week break between November 15 and November 30.

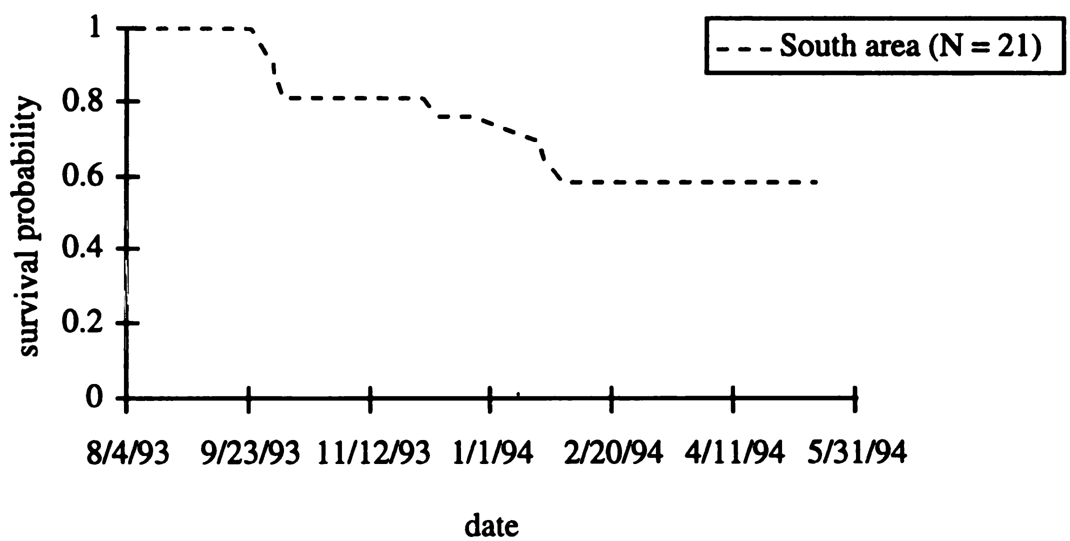


Figure 12. Survival probability for ruffed grouse radio-collared in the South area of the PRCSF closed site in 1993.

in 1993.

In the closed site in 1994, 52 birds were captured, of which 42 were collared. Four birds from 1993 survived long enough to be included in the survival analysis for 1994, 2 of which were captured and recollared, and are included in the total number of 42 collared birds. One bird that died of suffocation from the radio-collar, 1 that was killed by an avian predator, and 2 that had their radio-collars removed (all within 5 days of capture) were not used in the survival analysis. A total of 40 birds were used in the survival analysis. Survival probability was calculated as 0.38 (Figure 13), substantially lower than in 1993. In 1994, there was no significant difference in survival probabilities between the sites (Log rank, $p > 0.10$). Separating the closed site, 14 birds in the North area had a survival probability of 0.36, similar to the value of 0.38 in the South area (Figure 14).

In wildlife populations which are hunted, there is always the question as to whether hunting is additive or compensatory to natural mortality. If hunting is additive, it is in addition to natural deaths, and would impact overall mortality. Compensatory mortality takes the place of natural mortality, and so would not impact overall survival across the entire year. The significant difference in survival in 1993 may be due to low numbers of birds present on the sites. However, when population numbers are small, hunting may have a higher impact on survival. To understand the impacts of hunting versus other types of mortality, it is necessary to further examine the specific causes of mortality between sites.

Of the birds which were used in the open site survival analysis in 1993, 9.7% were alive on May 15 of 1994 (Table 28). The majority of the birds in the open site (32.3%)

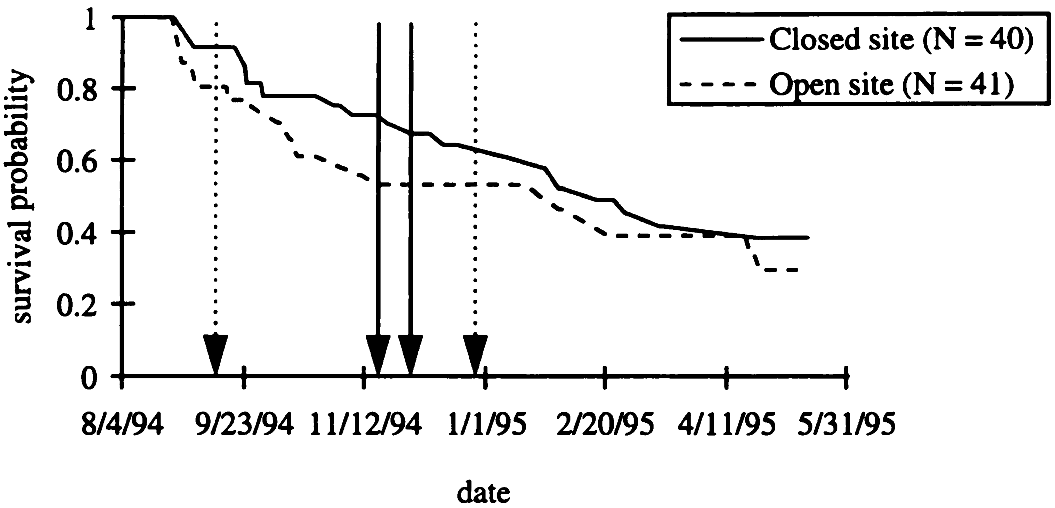


Figure 13. Survival probability for ruffed grouse radio-collared in the PRCSF in 1994. Arrows approximate hunting season, September 15 through December 31, with a 2 week break between November 15 and November 30.

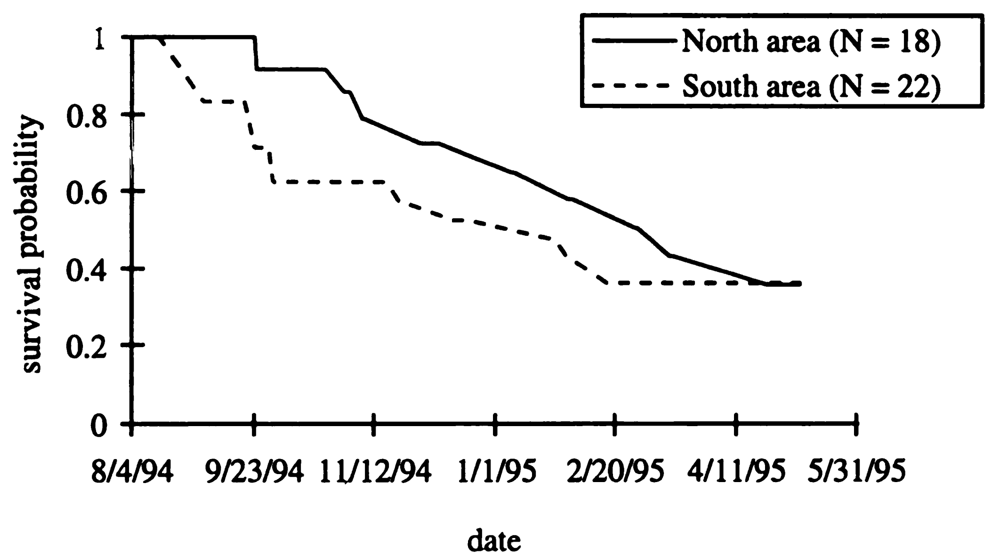


Figure 14. Survival probability for ruffed grouse radio-collared in the North and South areas of the PRCSF closed site in 1994.

Table 28. Number and percent of radio-collared ruffed grouse by status in the PRCSF open and closed sites in 1993 and 1994, as of May 15 of the following year. This table contains only birds which were used in the analysis of survival.

	1993				1994			
	Open site		Closed site		Open site		Closed site	
	N	%	N	%	N	%	N	%
Alive	3	9.7%	10	41.6%	6	14.6%	10	25.0%
Dead	19	61.6%	8	33.3%	19	46.3%	17	42.5%
Shot/collected	4	12.9%	0	0.0%	5	12.2%	0	0.0%
Shot/not collected	2	6.5%	0	0.0%	0	0.0%	0	0.0%
Avian predator	10	32.3%	3	12.5%	9	22.0%	11	27.5%
Mammalian predator	2	6.5%	2	8.3%	2	4.9%	2	5.0%
Illness	1	3.2%	1	4.2%	0	0.0%	0	0.0%
Unknown	0	0.0%	2	8.3%	3	7.3%	4	10.0%
Censored	9	29.0%	6	25.0%	16	39.0%	13	32.5%

Table 29. Number and percent of known deaths by category in the open and closed sites of the PRCSF in 1993 and 1994. No significant differences were detected in non-hunting mortalities between sites within the same year (Chi-square, $p > 0.10$).

	1993				1994			
	Open site		Closed site		Open site		Closed site	
	N	%	N	%	N	%	N	%
Shot/collected	4	21.1%	0	0.0%	5	26.3%	0	0.0%
Shot/not collected	2	10.5%	0	0.0%	0	0.0%	0	0.0%
Avian predator	10	52.6%	3	37.5%	9	47.4%	11	64.7%
Mammalian predator	2	10.5%	2	25.0%	2	10.5%	2	11.8%
Illness	1	5.3%	1	12.5%	0	0.0%	0	0.0%
Unknown	0	0.0%	2	25.0%	3	15.8%	4	23.5%

were killed by avian predators. Counting birds which had been shot, retrieved and returned by hunters, and those which were shot by hunters and retrieved by researchers, hunting mortalities accounted for 19.4% of birds in the open site. In the closed site, 41.6% of birds used in the survival analysis survived to May 15, 1994 (Table 28). Avian predators took 12.5% of birds, while mammalian predators took 8.3%.

By May 15, 1995, 14.3% of birds collared in 1994 in the open site were still alive. Hunting mortalities accounted for 11.9% of birds collared, slightly less than the 1993 value. The rate of avian predation was slightly lower, but still accounted for the majority of the uncensored birds (21.4%). In the closed site, 25% survived until May 15, and 27.5% were taken by avian predators.

Hunting season begins on September 15 and lasts through December 31, with a 2 week break for firearm deer season (November 15 - 30). All birds which were taken by hunters were shot between September 15 and November 14. No collars were returned in December. There were no known mortalities due to hunting in the closed site in 1993 or in 1994. If there was any illegal taking of birds in the closed site, it would be expected that the number of censored birds would be higher than in the open site. However, percentages of censored birds were comparable between sites in 1993 and in 1994 (Table 28).

Numbers and percentages of known deaths by category, year and site were also inspected (Table 29). Hunting accounted for 31.6% of known deaths in the open site in 1993, and 26.3% in 1994. Across both sites and years, avian predation was the leading cause of mortality. No significant differences were detected in non-hunting mortalities

Table 30. Number and percent of known deaths by category in the North and South areas of the closed site of the PRCSF in 1994. No significant differences were detected in non-hunting mortalities between areas (Chi-square, p > 0.10).

	North area		South area	
	N	%	N	%
Shot/collected	0	0.0%	0	0.0%
Shot/not collected	0	0.0%	0	0.0%
Avian predator	5	62.5%	6	66.6%
Mammalian predator	0	0.0%	2	22.2%
Illness	0	0.0%	0	0.0%
Unknown	3	37.5%	1	11.1%

between sites (or areas of the closed site, Table 30) within the same year. If hunting was compensatory, there should have been a discrepancy between non-hunting mortalities between sites. Specifically, numbers of natural mortalities should have been lower in the site open to hunting. Although survival seems to have been lowered by such mortality in 1993, survival in 1994 does not seem to have been affected.

Small (1985) reported an average annual mortality rate of 73% for ruffed grouse on hunted areas, which is generally consistent with the results on our open site. In a study on hunting losses, Rusch et al. (1984) reported a mean band recovery rate of 24% from 1978 - 1981 for ruffed grouse in Wisconsin. This is slightly higher, but comparable to the rate of return on the open site. It had long been thought that harvest rates of upwards of 50% of fall population could be tolerated by grouse populations (Bump et al. 1947). However, loss of habitat in northern forests may make such rates dangerously high.

Keith and Rusch (1986) conclude that cyclic declines in Minnesota and Wisconsin ruffed grouse are consistently associated with the influx of raptors from Canada. Additionally, Small et al. (1991) found that predation by hawks and owls was nearly double that of hunting losses. Avian predators also accounted for the majority of mortality in our study sites, but the association with raptor migration is not known.

Examining mortality rates by sex and age category can be of value for population predictions. Survival was split between sex and age classes in both sites and both years (Figure 15- 22). In the open site in 1993, the survival of juvenile birds declined to 0 at about the end of January (Figure 15). This effect was probably due to the low sample size, and a large number of censored birds. Survival probability for adult birds was 0.19.

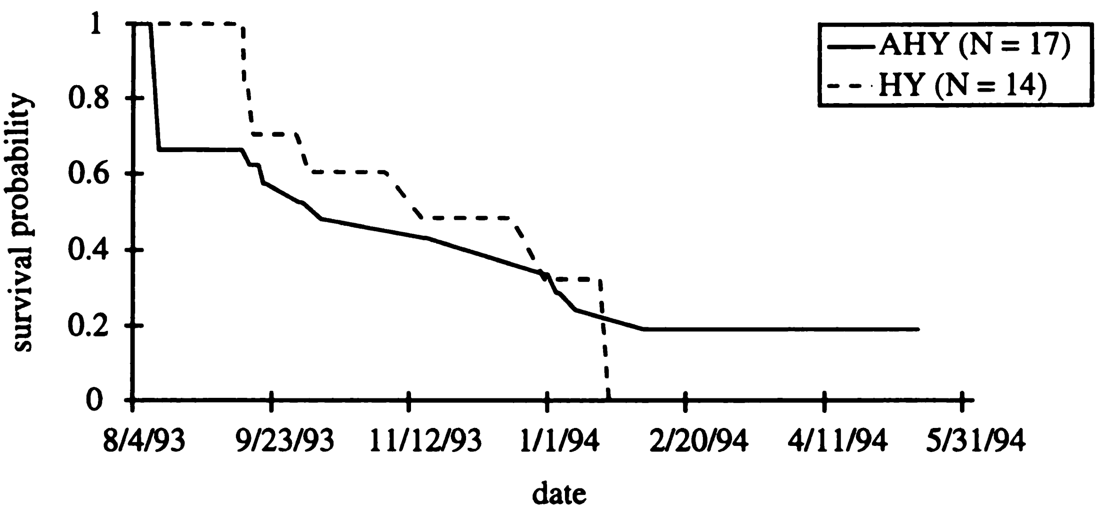


Figure 15. Survival probability for adult (AHY) and juvenile (HY) ruffed grouse in the open site of the PRCSF, 1993.

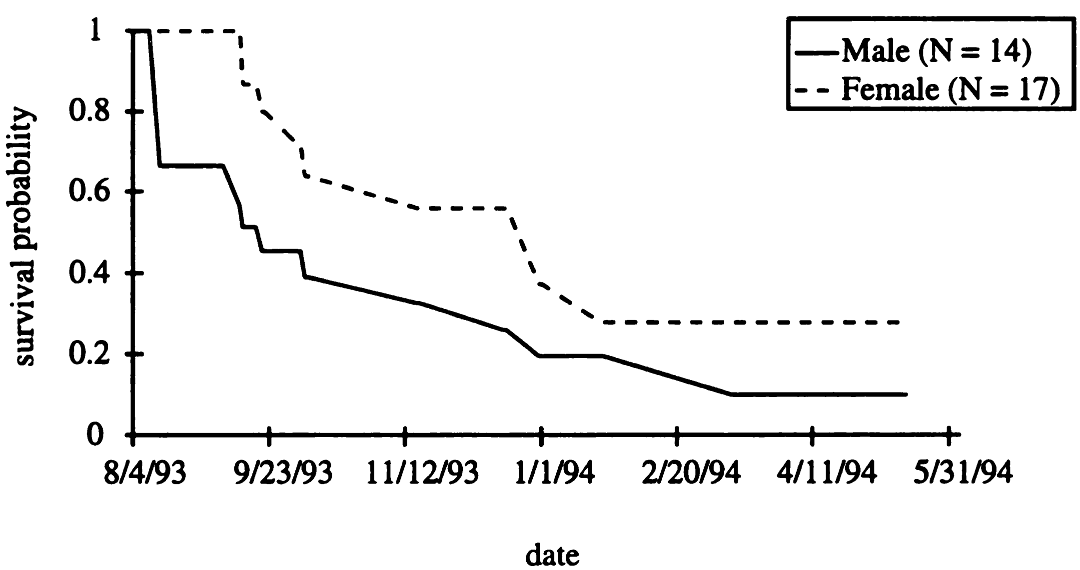


Figure 16. Survival probability for male and female ruffed grouse in the open site of the PRCSF, 1993.

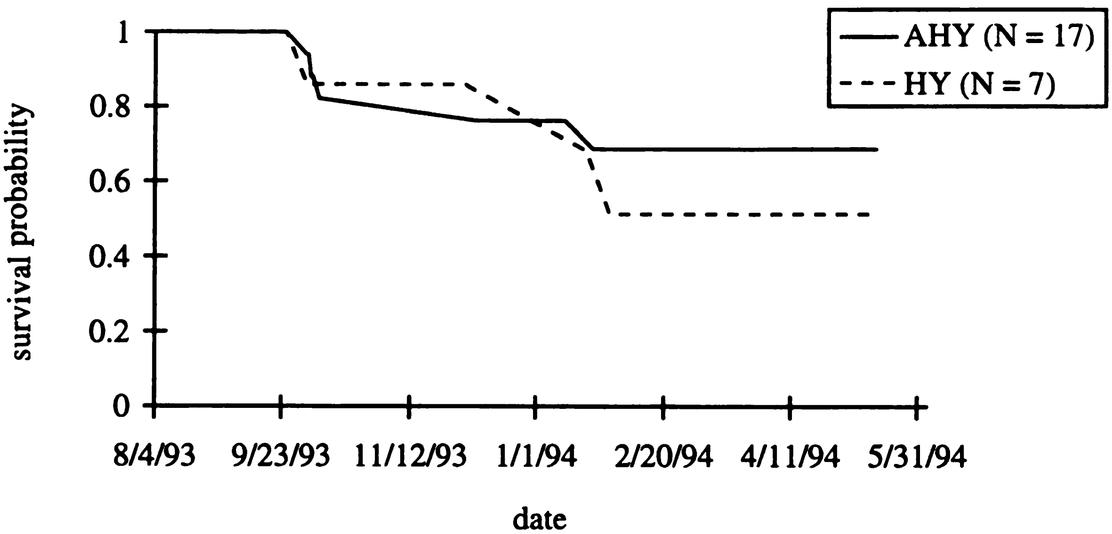


Figure 17. Survival probability for adult (AHY) and juvenile (HY) ruffed grouse in the closed site of the PRCSF, 1993.

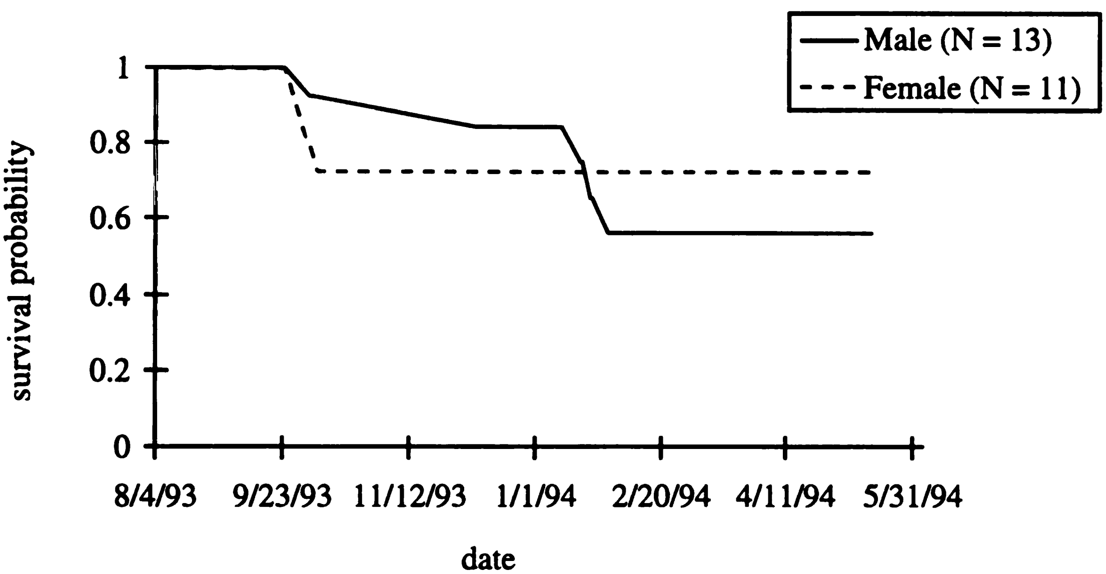


Figure 18. Survival probability for male and female ruffed grouse in the closed site of the PRCSF, 1993.

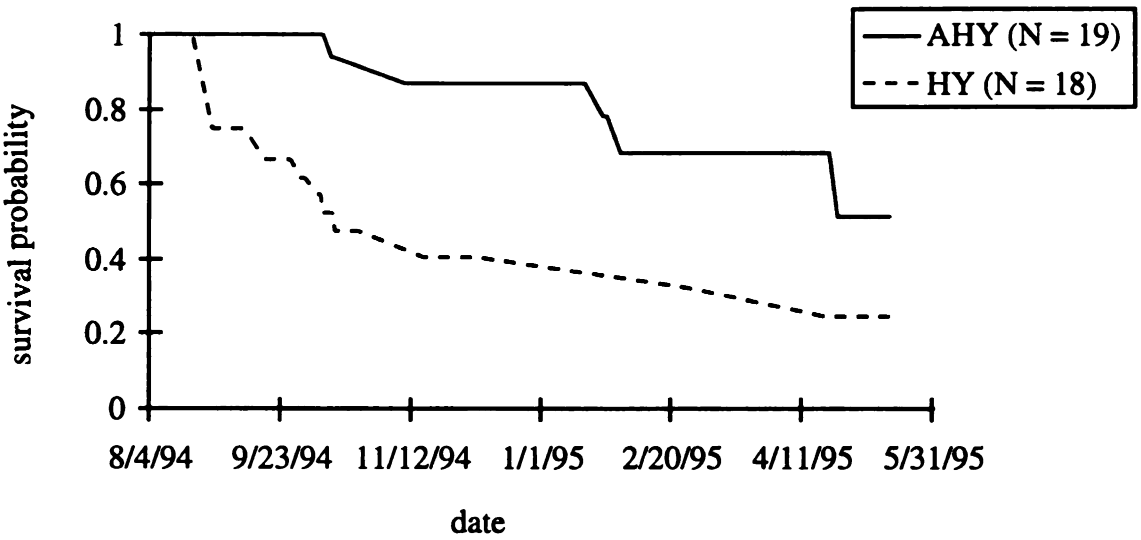


Figure 19. Survival probability for adult (AHY) and juvenile (HY) ruffed grouse in the open site of the PRCSF, 1994.

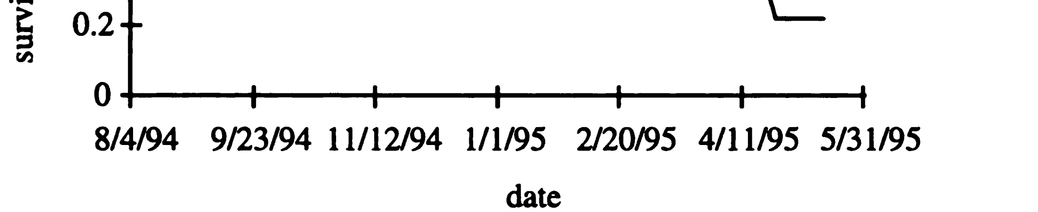


Figure 20. Survival probability for male and female ruffed grouse in the open site of the PRCSF, 1994.

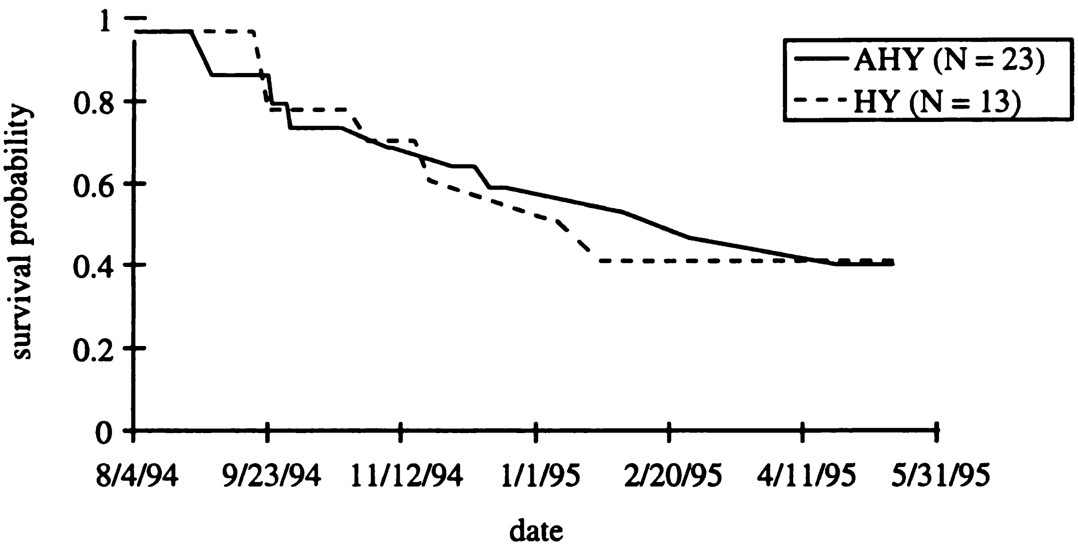


Figure 21. Survival probability for adult (AHY) and juvenile (HY) ruffed grouse in the closed site of the PRCSF, 1994.

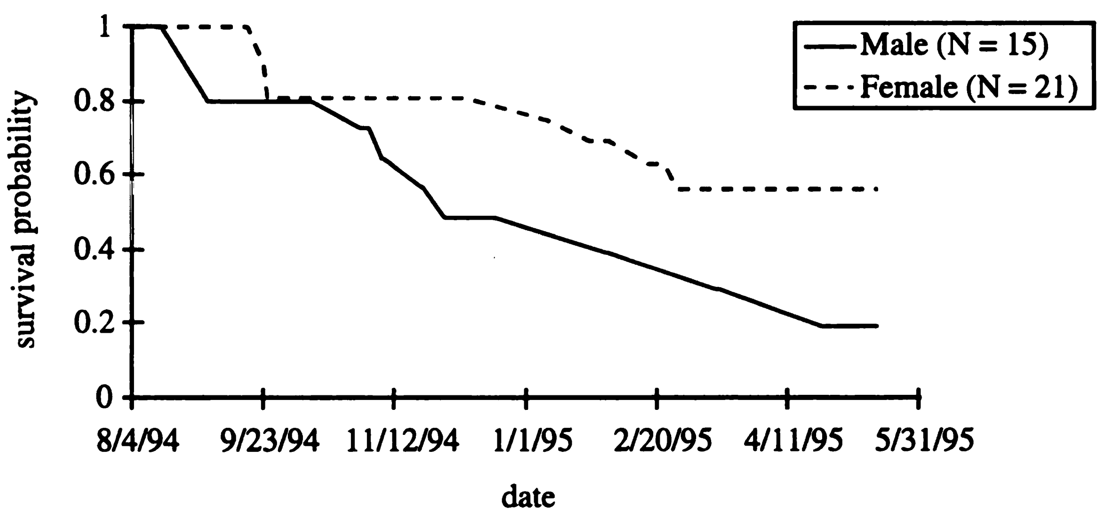


Figure 22. Survival probability for male and female ruffed grouse in the closed site of the PRCSF, 1994.

Female grouse (Figure 16) had a slightly higher survival probability (0.28) than males (0.10), but the curves were not significantly different (Log-rank, $p > 0.10$).

Closed site adults and juveniles had similar survival curves through most of the 1993 season (Figure 17), and ended with probabilities of 0.69 and 0.51. Male and female birds also had similar survival curves, with females at 0.73 and males at 0.56 (Figure 18). No significant differences were detected.

In 1994, open site adults had a survival probability of 0.51, much higher than the rate for juveniles, 0.24 (Figure 19). Survival probability was 0.41 for females (Figure 20), and 0.22 for males. Again, no significant differences were detected (Log-rank, $p > 0.10$).

In 1994 in the closed site, survival curves were fairly equal for adults and juveniles (Figure 21). However, survival probability was significantly higher for females (0.56) than for males (0.19) (Log-rank, $p < 0.10$) (Figure 22).

With the exception of the closed site juveniles in 1994, the trends of females and adults having higher survival rates were generally consistent and pronounced between sites within years. The lack of significant differences or the trends themselves may be due to small sample sizes. Some prior research has suggested that higher mortality rates of juveniles compared to adults are common in ruffed grouse (Gullion and Marshal 1968, Small et al. 1991), a difference which has generally been attributed to lack of experience (Small et al. 1991). However, other studies have failed to find significant differences in survival by sex or age class (Rusch and Keith 1971, DeStefano and Rusch 1986). The combination of yearly data (which has been done in the above mentioned studies) may be necessary for adequate reliability of the data.

Proportional hazards model

The Cox proportional hazards model (Cox 1972) was used to investigate the relationship between individual variables and survival. Because of low sample sizes within years, data from 1993 and 1994 were combined by site for the analysis.

Movement variables were not used in this analysis. There is an inherent bias involved in relating survival to movement variables, because a bird must survive long enough to detect trends in movement patterns (5 weeks in this study). Birds may have begun dispersal, and then been killed before their movements were detected as dispersal. Or, birds which were prone to one dispersal type may have been more vulnerable to mortality early in the season, causing their numbers to be underestimated. In future analyses, it may be possible to restructure movement variables to remove such biases.

Ten variables were used in the analysis: age; sex; condition index (proportion of weight to wing length); habitat use value * 100; and % locations in young, medium and old aspen, lowland conifers, lowland hardwoods, and old pine. The other habitat types had very few or no bird locations, and were not used in the analysis.

In the open site, the variables sex and habitat value had significant P values ($P < 0.10$) (Table 31). Risk of mortality was 40.1% higher for males than for females. For every 1 point increase in habitat use value, the risk increases 4.8%. There were no significant P values in the closed site.

Because it was found to be a significant variable in the open site, birds in each site were then stratified by sex, and the most probable proportional hazards models were found through stepwise regression. For entry into the model and to stay in the model, P

Table 31. Risk ratios and associated P values for individual variables tested for association to survival with the Cox Proportional Hazards Model (Cox 1972).

	Open site		Closed site	
	Risk ratio	P	Risk ratio	P
Age	0.664	0.188	0.927	0.831
Sex	0.599	0.087	0.813	0.584
Condition index	1.099	0.604	0.802	0.330
Habitat value	1.048	0.072	1.052	0.260
% Asp 1-10 yr.	1.006	0.667	0.970	0.209
% Asp 11-29 yr.	1.008	0.424	1.018	0.259
% Asp 30+ yr.	1.016	0.366	1.010	0.576
% Lowland hardwoods	0.986	0.575	0.920	0.141
% Lowland conifers	1.018	0.266	0.974	0.466
% Pine 30+ yr.	0.974	0.233	1.011	0.213
	N = 46		N = 46	

values were set at 0.20. For open site males, the variables age and % locations in aspen 11-29 years were selected by the model (Table 32). Juveniles had a risk of mortality 80.1% higher than adults, and risk increased 2.4% with each increase in percent of locations in medium aspen. In open site females, % locations in young and old aspen and lowland conifers were used in the model. For each increase in percent of locations in those habitat types, risk increased 9.4%, 13% and 18.1% respectively.

Age, and % locations in young and old aspen were found to fit the model for closed site males (Table 33). Juveniles had a risk of mortality 98.6% higher than adults, and risk decreased 14.8% for each point increase in percentage of locations in young aspen. In old aspen, however, risk increased 4.1% for each point increase in percentage of locations. In the model for closed site females, only one variable, % locations in pine > 30 years, was used. The risk of mortality increased 4.7% with each point increase in percentage of locations in old pine.

Age was found to be a significant variable in males in both sites, with juveniles having decreased survival. Some prior research, however, has shown that juveniles are not more vulnerable to mortality (DeStefano and Rusch 1986). In the aspen variables, results were also not as expected. In many cases, risk increased with % locations in various age classes of aspen. These results could be due to variability of habitat quality within individual aspen stands, or low sample size when age and sex categories were split within sites.

In a similar telemetry study, Vispo et al. (1995) measured habitat variables at flush sites of radiomarked grouse. Researchers used the Cox model to relate those variables to survival, and found presence of aspen and conifers to be associated with reduced

Table 32. Risk ratios and corresponding P values for explanatory variables found in a stepwise regression through the Cox proportional hazards model (Cox 1972), and overall model P values for male and female ruffed grouse in the open site of the PRCSF, 1993 and 1994.

	N	Risk ratio	P
Male			
Age		0.199	0.026
% locs. in aspen 11-29 yr.		1.024	0.062
Overall model	23		0.053
Female			
% locs. in aspen 1-10 yr.		1.094	0.121
% locs. in aspen 30+ yr.		1.130	0.086
% locs. in lowland conifers		1.181	0.003
Overall model	17		< 0.001

Table 33. Risk ratios and corresponding P values for explanatory variables found in a stepwise regression through the Cox proportional hazards model (Cox 1972), and overall model P values for male and female ruffed grouse in the closed site of the PRCSF, 1993 and 1994.

	N	Risk ratio	P
Male			
Age		0.014	0.007
% locs. in aspen 1-10 yr.		0.852	0.036
% locs. in aspen 30+ yr.		1.041	0.106
Overall model	21		0.002
Female			
% locs. pine 30+ yr.		1.047	0.081
Overall model	18		0.036

mortality. The presence of birch in the overstory was found to be associated with increased mortality. Such finely measured habitat variables may be the key to understanding why some broadly generalized variables have an unexpected effect.

Sample size was of major concern in model building. As the number of birds decreased with the splitting of categories, the number of events (deaths) decreased to a level where the data were not very reliable (e.g. the removal of a bird would dramatically change model output). This analysis should be considered exploratory, and further research is warranted. A similar analysis with more collared birds, and perhaps more detailed habitat use data would be extremely valuable.

Conclusions

Trapping success was generally low in both sites of the PRCSF, with the open site having slightly higher success in both years. More adults than juveniles were caught in 1993, but age and sex ratios of trapped birds did not differ between sites. Incidences of injuries or deaths related to trapping were minimal.

The open and closed sites were different in distribution of habitat types. The open site had higher percentages of aspen and hardwood types, while the closed was dominated by older pine, hardwoods and lowland conifers. The closed site was divided into the North and South areas for analysis, due to differences in habitat types across the landscape. Stands in the North area of the closed site were predominantly the older pine types, while the South area had large percentages of aspen, hardwoods and lowland conifers.

The quality of habitat in the open site was slightly higher than in the closed site in medium and older aged aspen stands, and in overall HSI value. Although it would be advantageous to the study for the sites to be of comparable quality, this imbalance is preferable to the alternative of the open site being of lower quality than the closed. In this way, if ruffed grouse survival is lower in the site open to hunting, it cannot be attributed to poorer habitat quality.

In the open site, medium aged aspen, lowland conifers and older aspen had the highest mean HSI values. In the closed site, young pine, lowland hardwoods and lowland conifers all had higher mean HSI values than medium aged aspen, which was expected to contribute the most to the overall value of the site. In both sites, conifer stems contributed significant amounts to the stem densities of most habitat types. Aspen stands were found to be generally lacking in stem densities of aspen, but the addition of conifer stems into the ESD (as called for in the model) brought many stands to the desired density.

Ruffed grouse in the Pigeon River showed 3 distinct movement patterns: Type I and Type II non-dispersers, and dispersers. Non-dispersers were separated into 2 types based on amount of movement during the fall. Type II non-dispersers showed increased movements during the traditional dispersal period, but had no distinct dispersal from one area to another. No consistent trends were found in the movements of ruffed grouse by site, sex or age class. Birds in this study dispersed considerably shorter distances and had smaller home ranges than found in other studies.

In the open site, birds seemed to show a preference for older aspen types. In the closed site, birds used openings, lowland hardwoods, older pine and aspen types more frequently than expected from their availability. Hardwood types were used very infrequently in both sites in both years. Habitat use values were significantly higher in the open site than in either area of the closed site in both years. Habitat use values for dispersers were consistently lower than those for non-dispersers in both sites in both years.

In 1993, there was a significant difference in survival between sites open and closed to hunting. No difference was detected in 1994. Most mortalities were due to avian predation, but hunting did play a significant role in survival in the open site in 1993. The rate of predation by mammals was low. Adult ruffed grouse had higher survival rates than juveniles, and females had higher survival rates than males.

The proportional hazards model showed different variables affecting survival between sexes and sites. Age was a factor in survival for males in both areas, with adults having a higher chance of survival than juveniles. Percent locations in aspen types were negatively related to survival in many cases, results which cannot be explained at this time. Old pine and lowland conifers were also negatively related to survival. The results of the proportional hazards model should be taken as preliminary and exploratory, and will not be taken into consideration for management implications.

Management Implications

In 1980, Hammill and Visser expressed concern that the aspen resource in Michigan has been on a steady decline since about 1935. A low demand for aspen products and natural succession to other species have been the main causes for the decline. They recommended that harvest rates increase, and private landowners be educated as to the value of aspen as a wildlife resource. The open site of the PRCSF has moderate acreages of aspen, but the closed site (especially the North area) is lacking stands of this type. Additionally, although older aspen continues to be of value for grouse after its rotational age in the open site, older aspen in the closed site seems to lack adequate stem densities. Unless cutting is increased, acreages of medium aged aspen will continue to decline, and succeed to other types of lesser quality.

Managing aspen for ruffed grouse may be in conflict with some of the specific management goals for the Pigeon River Forest. These goals include: 1) providing favorable habitat for elk; 2) furnishing food, cover and seclusion for wildlife; and 3) providing recreational opportunities for people in keeping with the quiet, peaceful and wild character of the area. Management options must be weighed, considering the benefits versus the consequences to other wildlife and land uses. If it is within the interests of the forest to sustain or increase ruffed grouse habitat, it is recommended that cutting be increased in the North area of the closed site, and continue at the current rate in other areas of the forest.

Ungulate browsing has been shown to have a thinning effect on regenerating aspen stands in the PRCSF (Campa et al. 1993), and the quality of aspen for ruffed grouse may be a reflection of this thinning. Therefore, when aspen stands are cut with the intention of improving ruffed grouse habitat, attention should be paid to adjacent habitats, ungulate densities in the area, site quality, and size of the cut. Although traditional ruffed grouse management practices have stressed small cuts (< 10 acres) (Gullion 1984), the presence of heavy ungulate browsing in the Pigeon may render small cuts inadequate. Larger cuts (> 100 acres) may be able to sustain heavy browsing pressure on the edges, while providing adequate ruffed grouse cover in the center. It may not be possible to provide adequate aspen habitat for ruffed grouse throughout the Pigeon River area, but grouse management areas away from high ungulate concentrations may be an alternative.

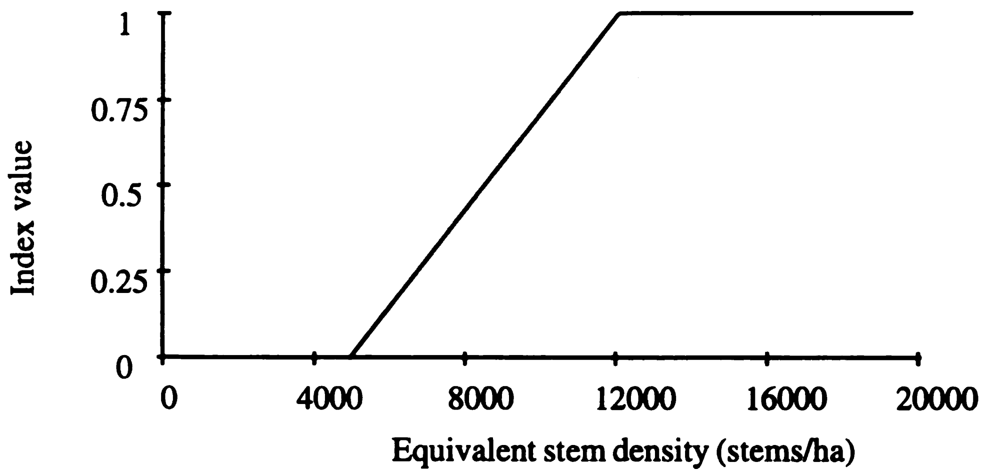
The importance of medium aged aspen stems for ruffed grouse in the northern United States cannot be argued. However, many ruffed grouse in the Pigeon River Country State Forest make use of other habitat types which are not usually considered productive grouse habitat. Lowland hardwoods and pine types (with developed understories) provide adequate habitat for grouse in the closed site. When considering management on a landscape level, it would be beneficial to plan such areas to be in proximity to aspen types. A plan which takes into account the interspersion of forest types may decrease the probability that dispersing birds must move through poor habitat, thereby possibly increasing their chances for survival.

Historically, control of grouse populations has been by extreme changes in the hunting regulations. Throughout the northern United States populations have continued to cycle. The difference in survival between sites in 1993, however, may indicate that hunting has an adverse affect when populations are at their lowest points. Since the trends of the cycle are known, it may benefit populations to moderately limit hunting for a year prior to and during the low point of the cycle. Decreasing bag limits alone will not substantially change the number of birds harvested, but shortening the season, decreasing bag limits and educating hunters should.

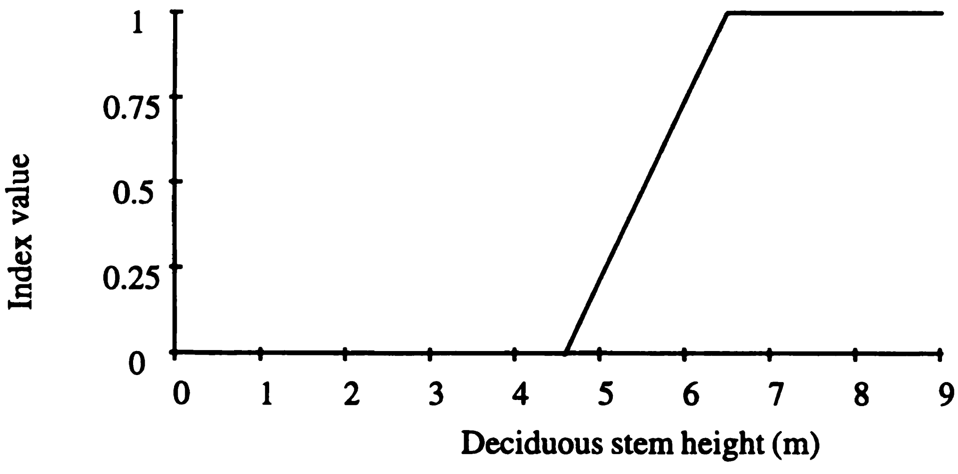
In Michigan, it is widely believed that hunting in December is responsible for a large percentage of total birds taken. In this study, no collars were returned by hunters in December in either year. It is not recommended that a shortening of the season take place in December, but rather in the season before November 15. If this takes place in conjunction with a coordinated effort to encourage hunters to limit their time afield, the low points of the cycle may not be as extreme. The possibility of a quicker recovery of the population should encourage compliance and cooperation.

APPENDICES

Appendix I. Production functions from the Habitat Model for Ruffed Grouse in Michigan (Hammill and Moran 1986).

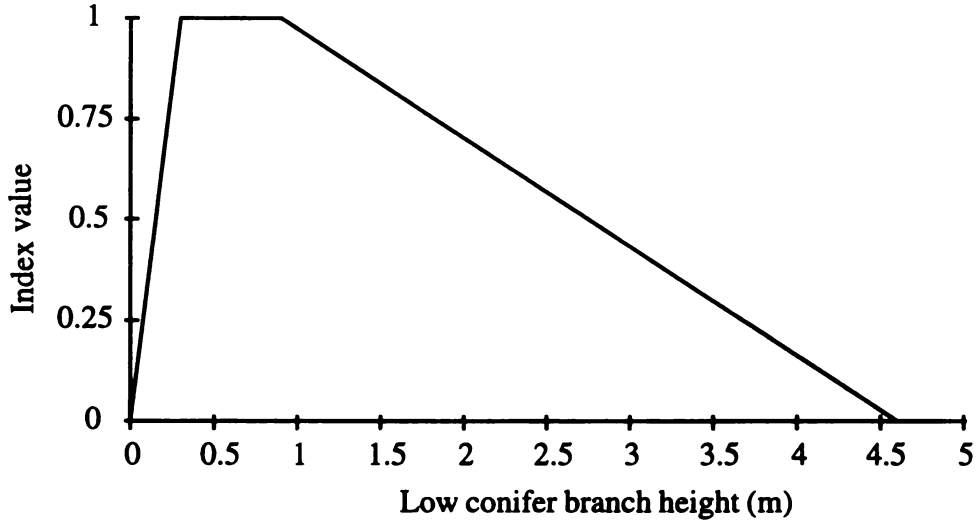


Appendix I, Figure 1. Index value for equivalent stem density in the Michigan model.

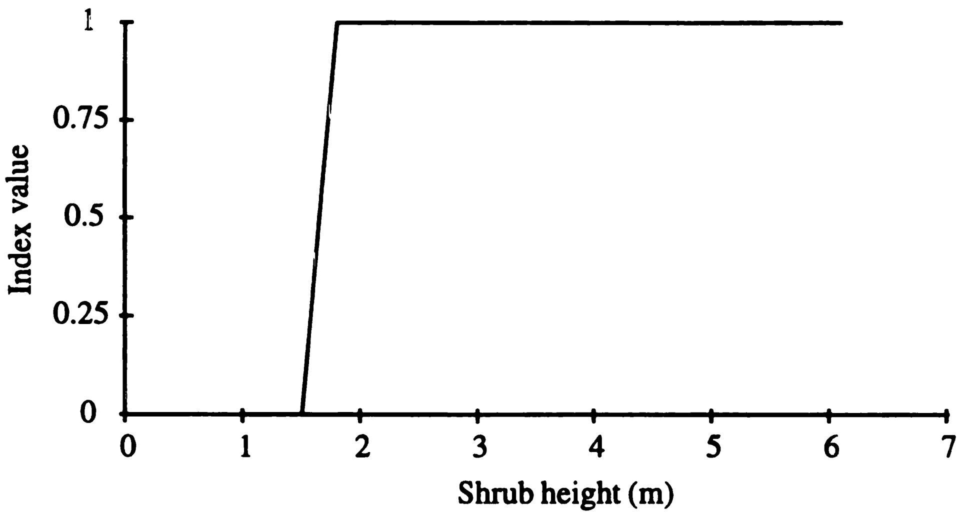


Appendix I, Figure 2. Index value for average height of deciduous trees in the Michigan model.

Appendix I. (cont'd)

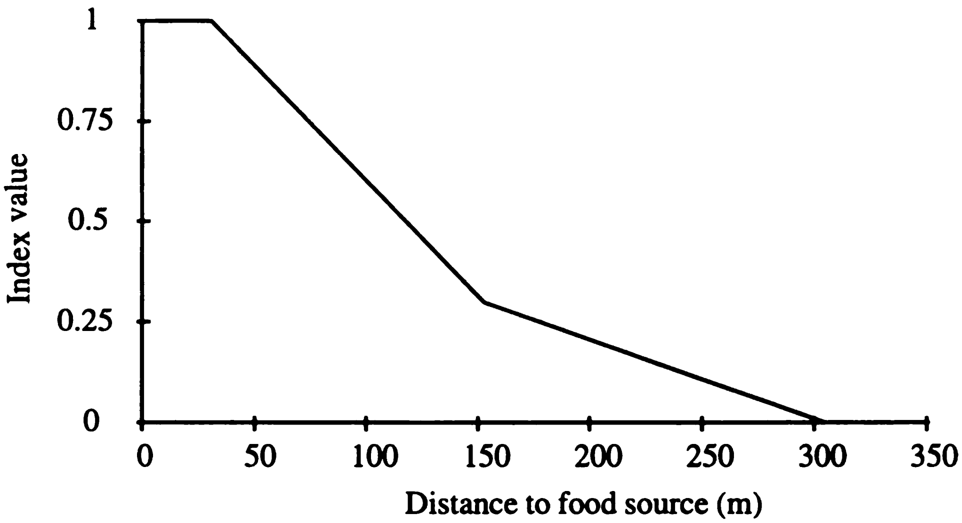


Appendix I, Figure 3. Index value for height above ground of lower coniferous branches in the Michigan model.



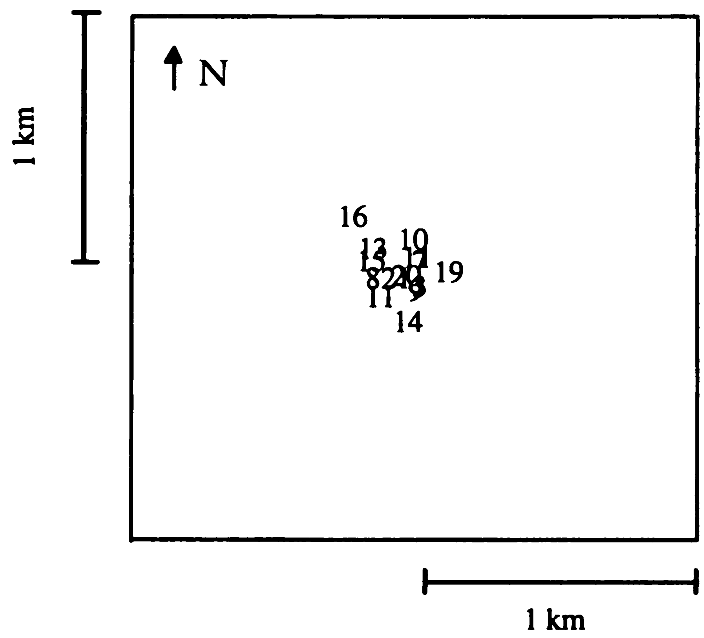
Appendix I, Figure 4. Index value for average height of deciduous shrubs in the Michigan model.

Appendix I. (cont'd)

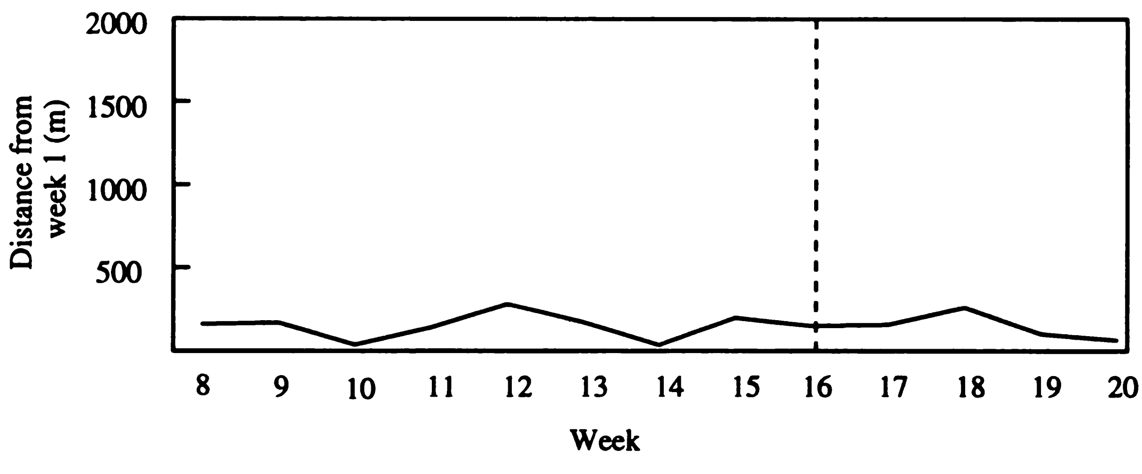


Appendix I, Figure 5. Index value for distance between life requisites in the Michigan model.

Appendix II. Examples of ruffed grouse dispersal patterns in Pigeon River Country State Forest, 1993.

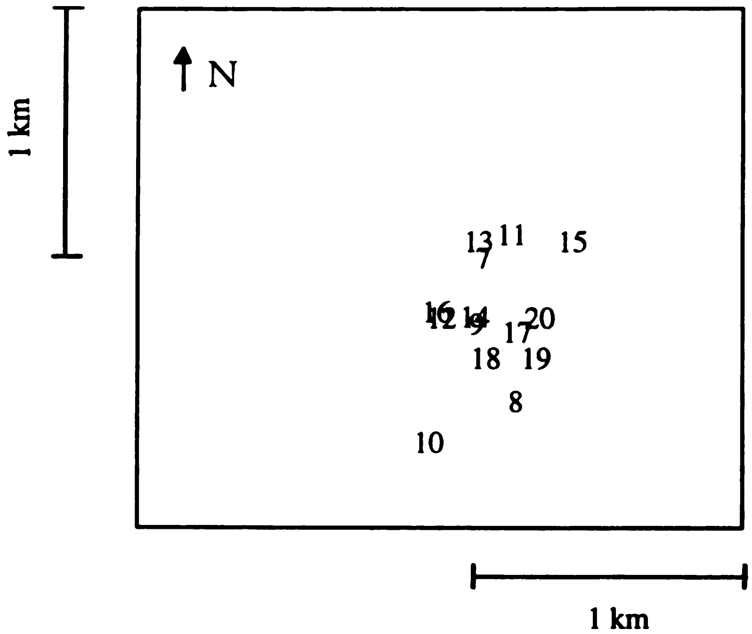


Appendix II, Figure 1. Weekly harmonic centers for a single bird plotted spatially and numbered by week. This bird was categorized as a Type I non-disperser.

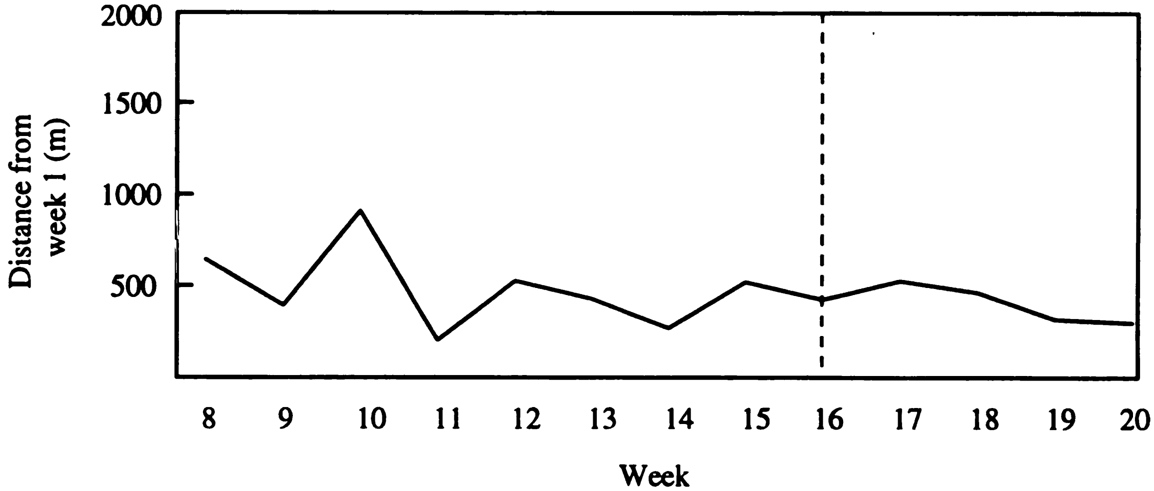


Appendix II, Figure 2. Distance moved by a single bird from the harmonic center of its locations during the first week located to the harmonic center of each following week. This bird was categorized as a Type I non-disperser (same individual as in Appendix II, Figure 1). Numbers indicate weeks, with week 1 = August 1 - August 7. Dashed line at week 16 indicates November 30, after which movements are not considered fall dispersal.

Appendix II. (Cont'd)

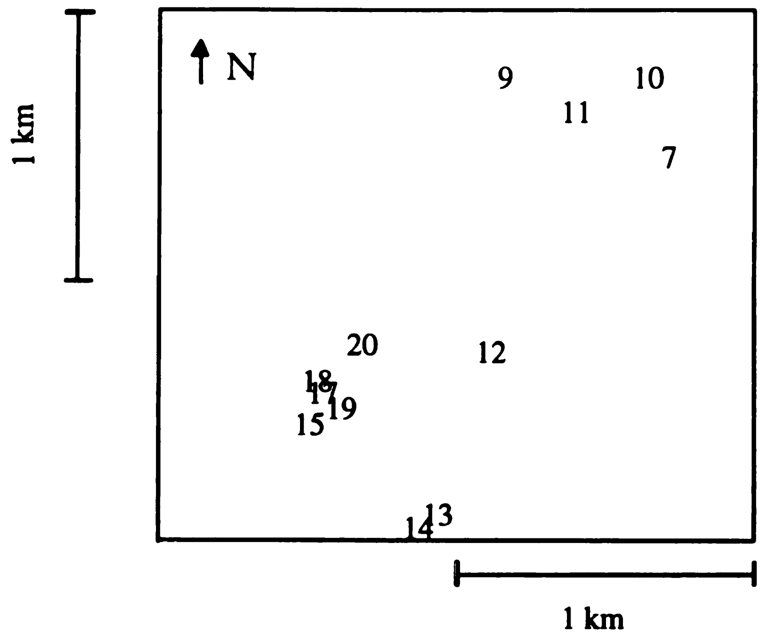


Appendix II, Figure 3. Weekly harmonic centers for a single bird plotted spatially and numbered by week. This bird was categorized as a Type II non-disperser.

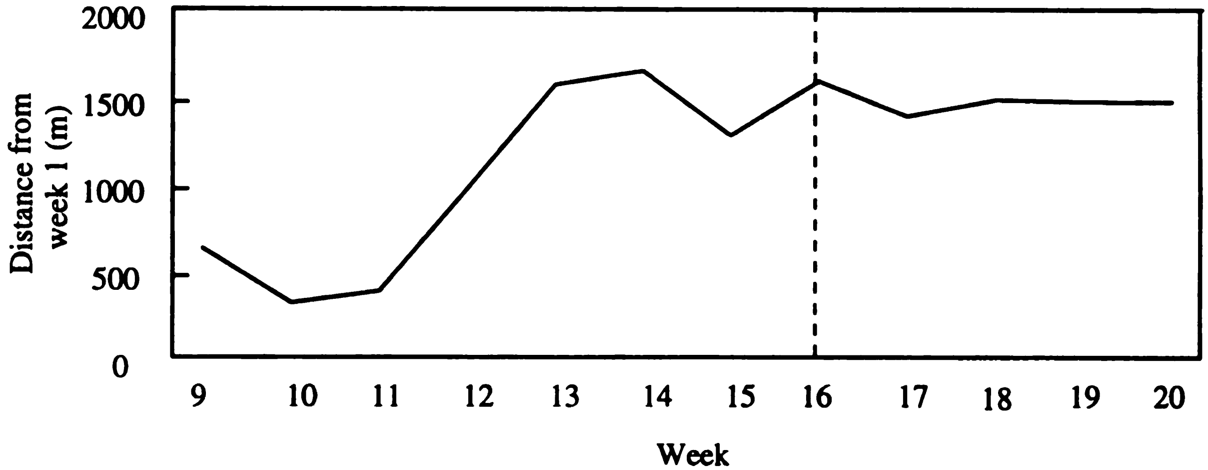


Appendix II, Figure 4. Distance moved by a single bird from the harmonic center of its locations during the first week located to the harmonic center of each following week. This bird was categorized as a Type II non-disperser (same individual as in Appendix II, Figure 3). Numbers indicate weeks, with week 1 = August 1 - August 7. Dashed line at week 16 indicates November 30, after which movements are not considered fall dispersal.

Appendix II. (Cont'd)

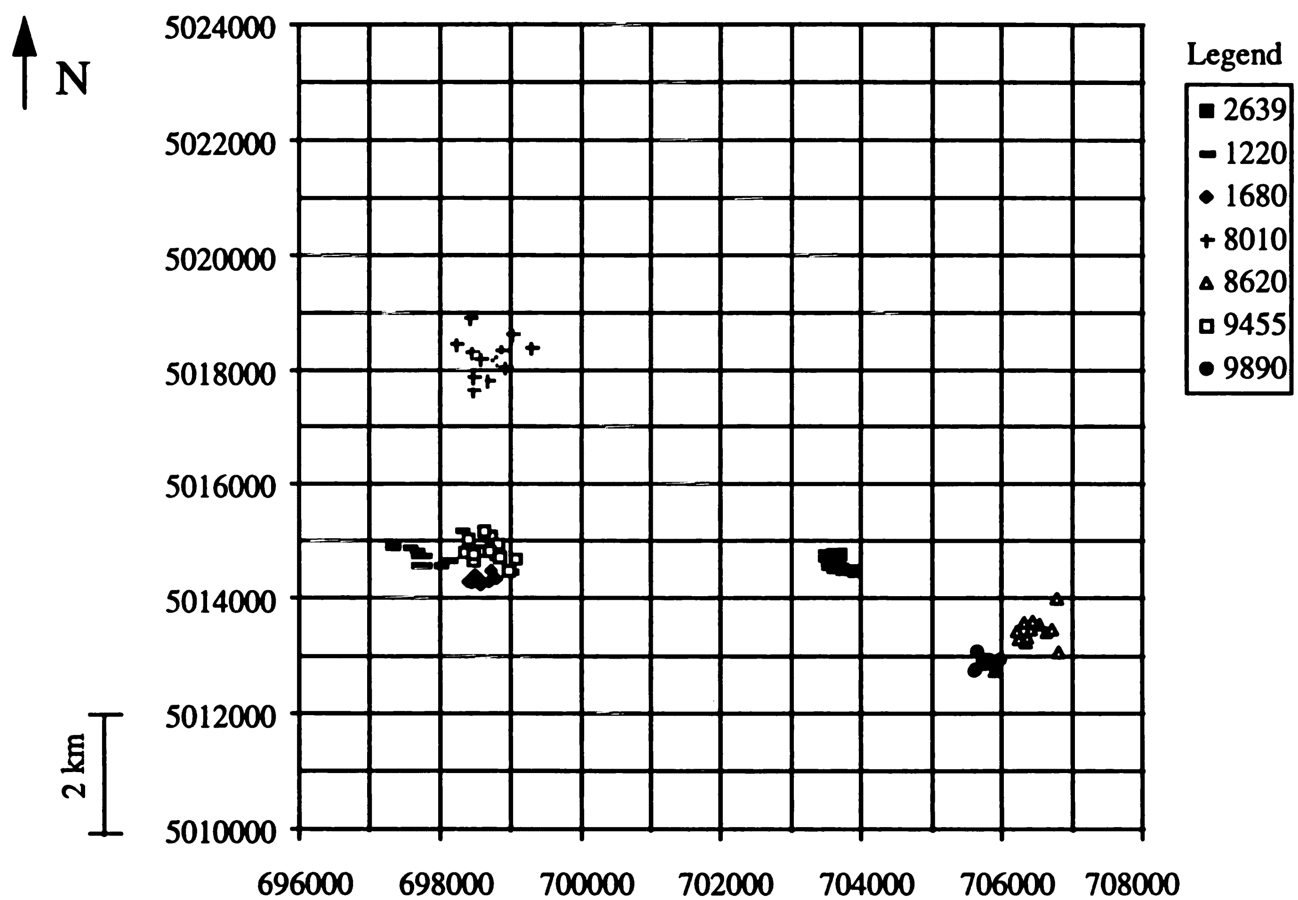


Appendix II, Figure 5. Weekly harmonic centers for a single bird plotted spatially and numbered by week. This bird was categorized as a disperser.



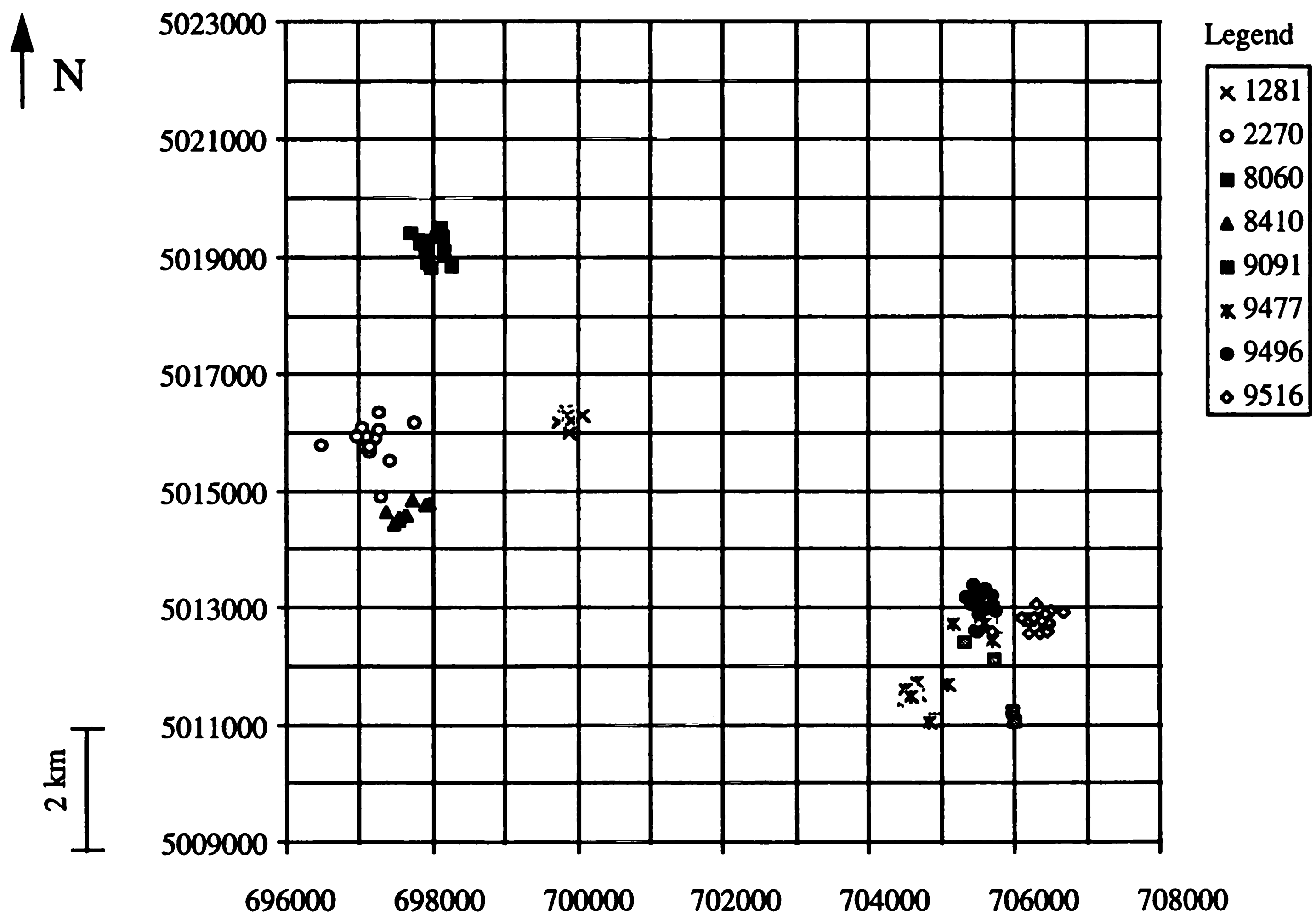
Appendix II, Figure 6. Distance moved by a single bird from the harmonic center of its locations during the first week located to the harmonic center of each following week. This bird was categorized as a disperser (same individual as in Appendix II,Figure 5). Numbers indicate weeks, with week 1 = August 1 - August 7. Dashed line at week 16 indicates November 30, after which movements are not considered fall dispersal.

Appendix III. Weekly harmonic centers of individual ruffed grouse in the open and closed sites of the Pigeon River Country State Forest, in 1993 and 1994.



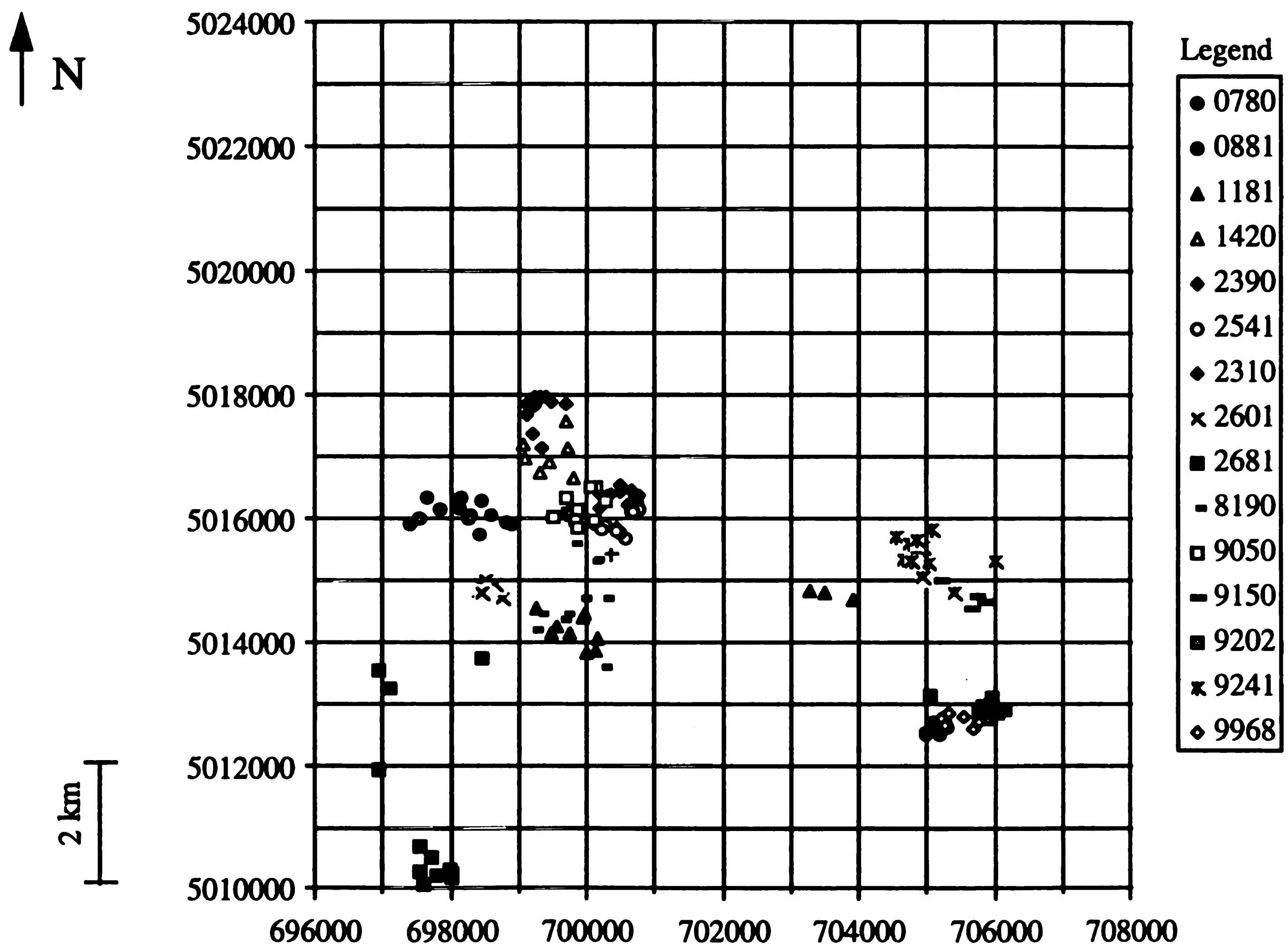
Appendix III, Figure 1. Weekly harmonic centers for individual male ruffed grouse (identified by radio frequency) in the open site of the PRCSF, September - December, 1993. Map is scaled with Universal Transverse Mercator (UTM) coordinates.

Appendix III. (cont'd)



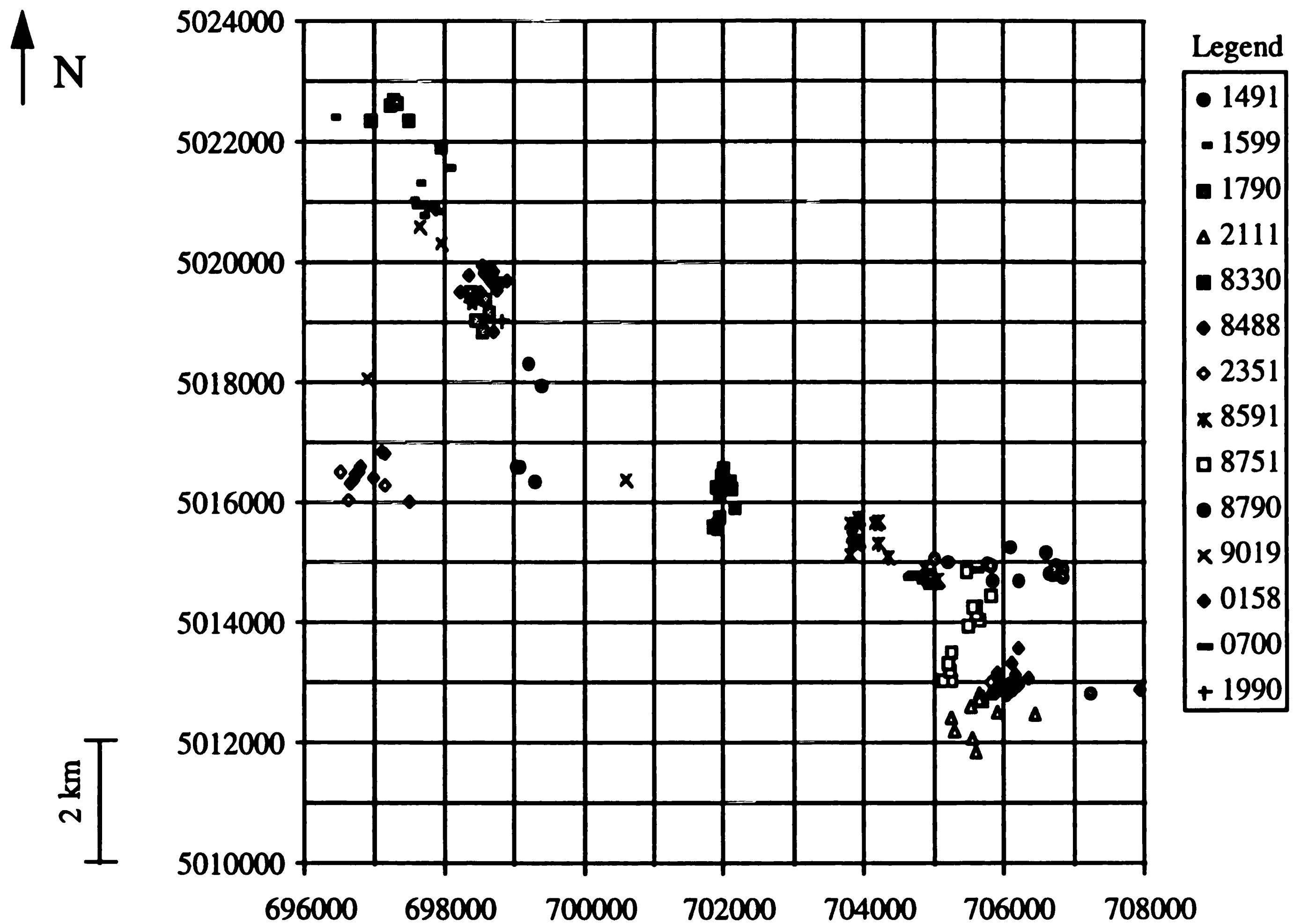
Appendix III, Figure 2. Weekly harmonic centers for individual female ruffed grouse (identified by radio frequency) in the open site of the PRCSF, September - December, 1993. Map is scaled with Universal Transverse Mercator (UTM) coordinates.

Appendix III. (cont'd)



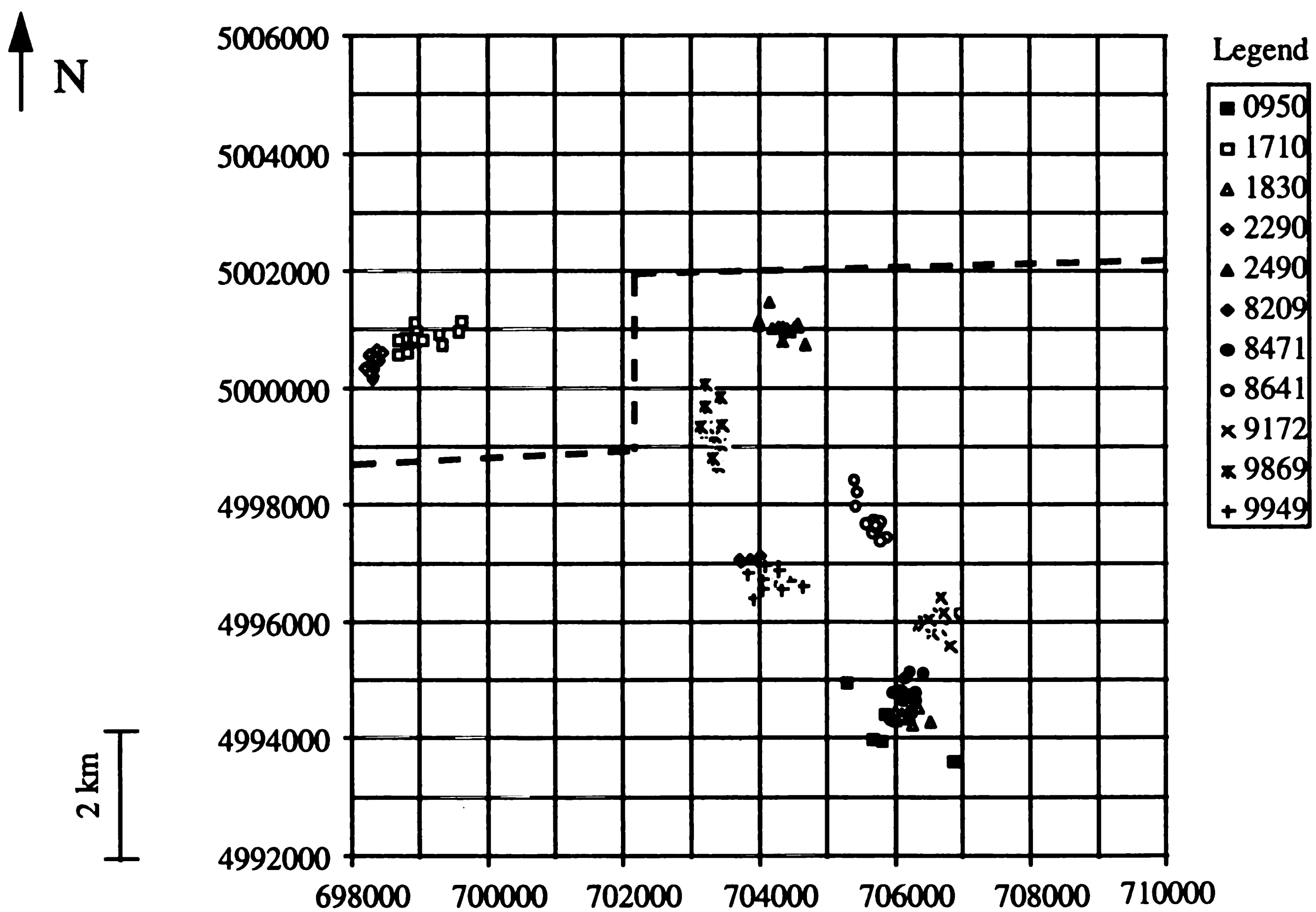
Appendix III, Figure 3. Weekly harmonic centers for individual male ruffed grouse (identified by radio-frequency) in the open site of the PRCSF, August - December, 1994. Map is scaled with Universal Transverse Mercator (UTM) coordinates.

Appendix III. (cont'd)



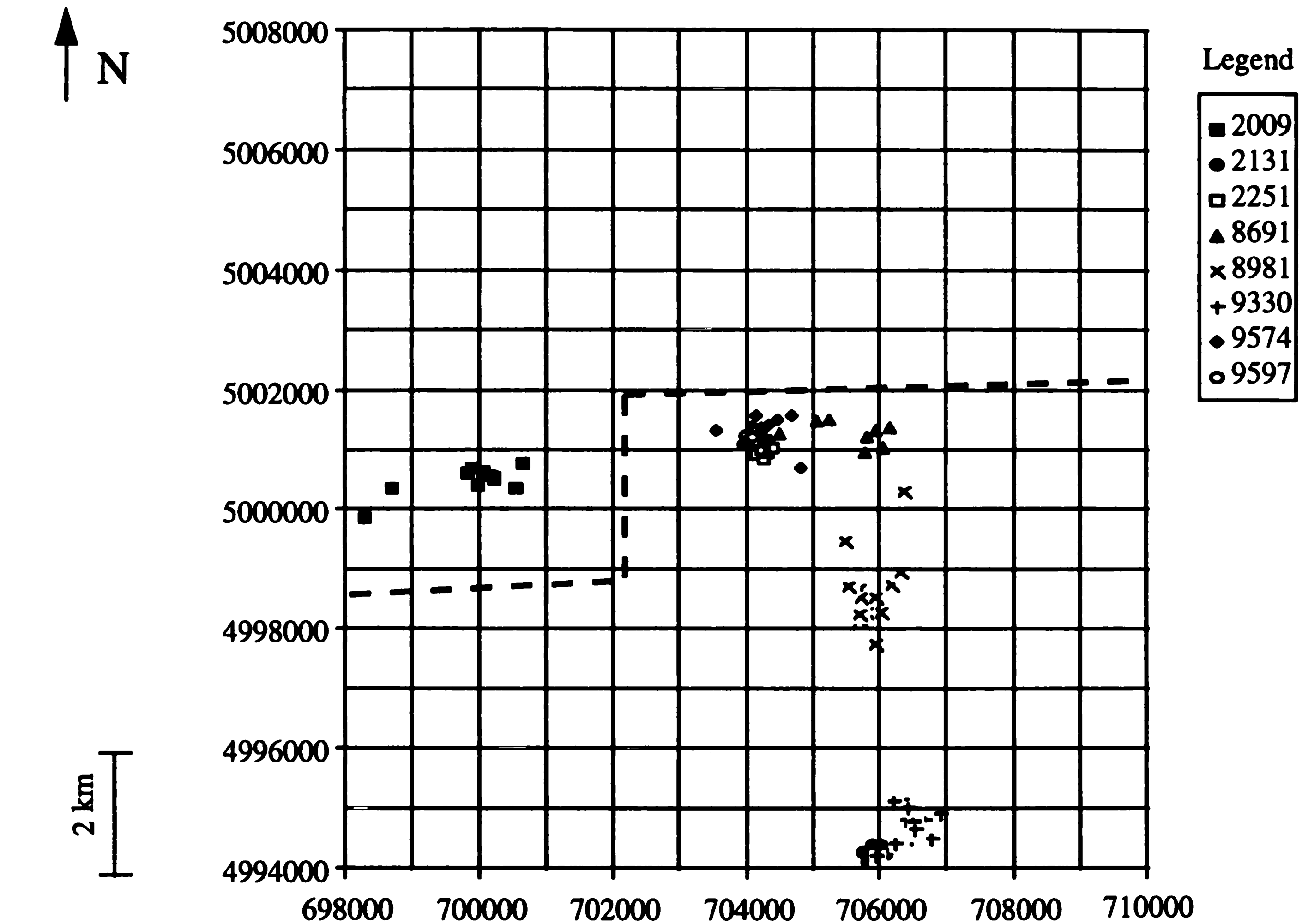
Appendix III, Figure 4. Weekly harmonic centers of individual female and unknown sex ruffed grouse (identified by radio-frequency) in the open site of the PRCSF, August - December, 1994. Map is scaled with Universal Transverse Mercator (UTM) coordinates.

Appendix III. (cont'd)



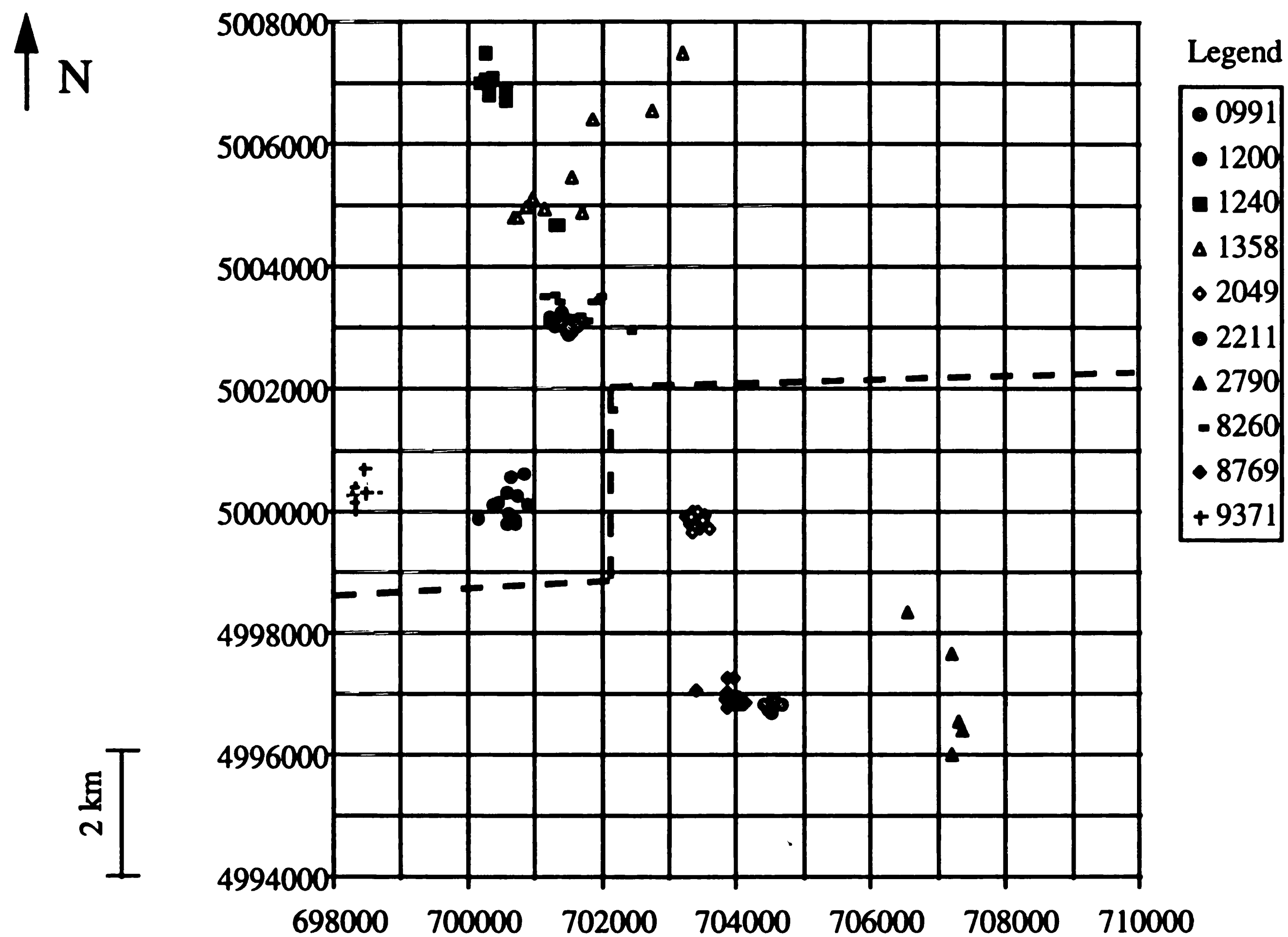
Appendix III, Figure 5. Weekly harmonic centers for individual male ruffed grouse (identified by radio frequency) in the closed site of the PRCSF, September - December, 1993. Map is scaled with Universal Transverse Mercator (UTM) coordinates. Dashed line indicates the approximate location of the division between the North and South areas of the closed site.

Appendix III. (cont'd)



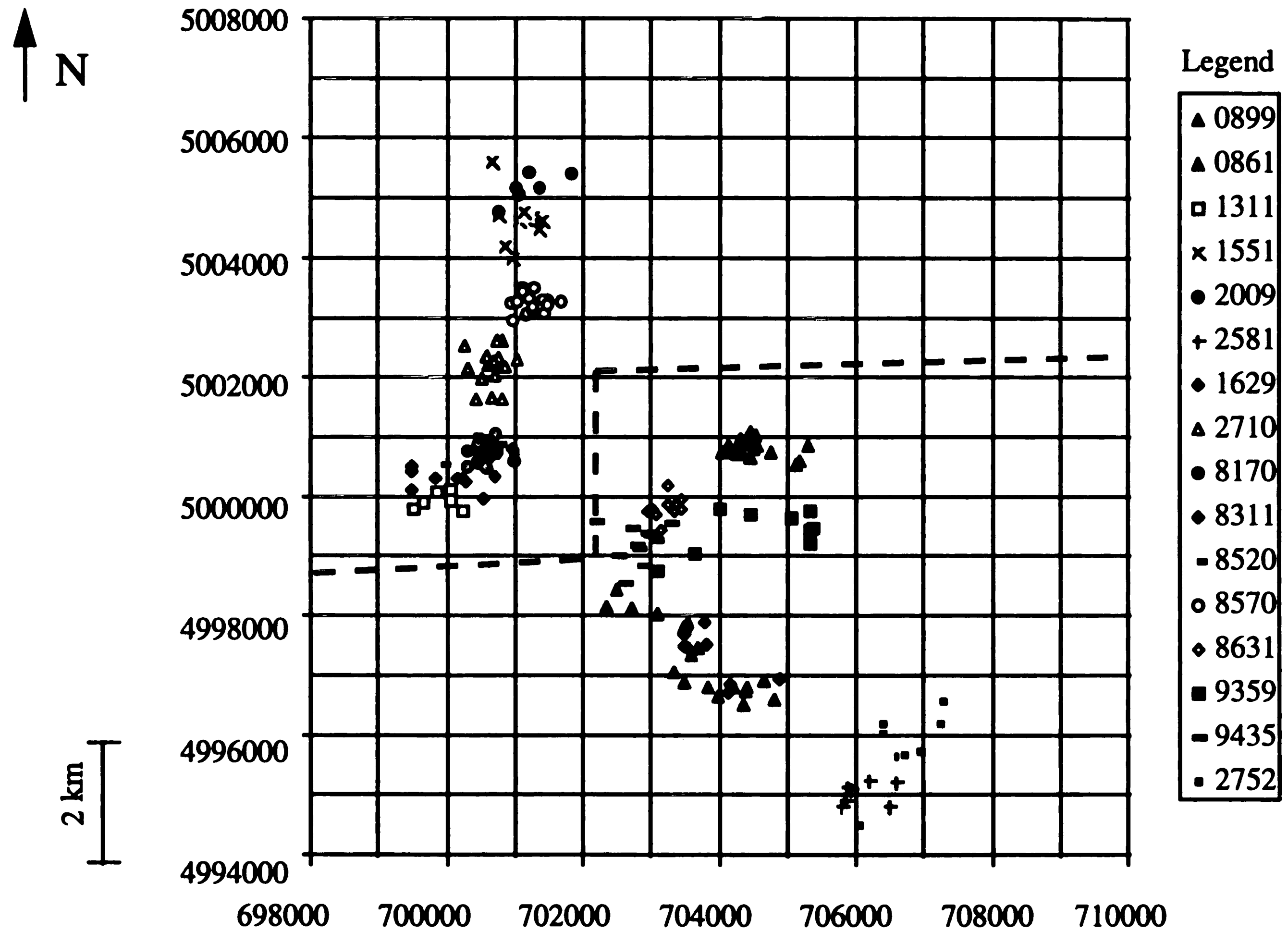
Appendix III, Figure 6. Weekly harmonic centers for individual female ruffed grouse (identified by radio-frequency) in the closed site of the PRCSF, September - December, 1993. Map is scaled with Universal Transverse Mercator (UTM) coordinates. Dashed line indicates the approximate location of the division between the North and South areas of the closed site.

Appendix III. (cont'd)



Appendix III, Figure 7. Weekly harmonic centers for individual male ruffed grouse (identified by radio frequency) in the closed site ofthe PRCSF, August - December, 1994. Map is scaled with Universal Transverse Mercator (UTM) coordinates. Dashed line indicates the approximate location of the division between the North and South areas of the closed site.

Appendix III. (cont'd)



Appendix III, Figure 8. Weekly harmonic centers for female and unknown sex ruffed grouse (identified by radio frequency) in the closed site of the PRCSF, August - December, 1994. Map is scaled with Universal Transverse Mercator (UTM) coordinates. Dashed line indicates approximate location of the division between the North and South areas of the closed site.

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