NESTING SUCCESS AND CHICK SURVIVAL OF RUFFED GROUSE (BONASA UMBELLUS) IN NORTHERN MICHIGAN

By

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A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Fisheries and Wildlife

1998

ABSTRACT

NESTING SUCCESS AND CHICK SURVIVAL OF RUFFED GROUSE (BONASA UMBELLUS) IN NORTHERN MICHIGAN

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Although much is known about the breeding and brooding behavior of ruffed grouse (*Bonasa umbellus*) hens, relatively little is known about the fate of their nests and chicks. This study was designed to document the reproductive parameters related to nesting and quantify nest site characteristics by monitoring the nests of radio-marked grouse hens in 1996 and 1997. Also, miniature radio transmitters were used to determine the predispersal survival rate of grouse chicks.

First nesting attempts had a lower Mayfield survival rate (47.8%), a higher mean clutch size (12.7 eggs), and higher egg hatchability (95.9%) than did second nesting attempts (80.3% nest survival, 7.3 eggs/clutch, and 83.3% hatchability). The median hatching dates were 10 June for first nests and 1 July for second nests. Nest site characteristics were highly variable. Chick survival to 7 September was approximately 32%, and an estimated 2.25 juvenile grouse were recruited into the fall population for each hen that began nesting the previous spring.

ACKNOWLEDGMENTS

Many people in several organizations helped with the completion of this research project. I would like to begin by thanking Dr. Scott Winterstein, my major professor and the principle investigator on the Michigan Ruffed Grouse Research Project, for his guidance throughout my degree program. My other graduate committee members, Dr. Rique Campa and Dr. Don Beaver, were valuable advisors as well. I would like to thank my graduate student colleagues on the grouse project; Meg Clark for valuable assistance throughout my program and Allison Gormley for helping to get me oriented in the beginning. I am indebted to my interns who conducted most of the field work directly related to this thesis. They were Steve Niemela, Mike VanAntwerp, Erynn Call, and Bill Dodge. Many others helped with field work, especially Jeff Breuker, Ursula Rosauer, Matt Carmer, and Andrew Larder.

Michigan Department of Natural Resources personnel helped with various aspects of the project, especially Larry Robinson and Dan Soults from the Mio office, Bill Green from the Roscommon office, and Tom Cooley from Rose Lake Wildlife Research Area. United States Forest Service biologists Dave Regal and Phil Huber helped me gather information about vegetation. Special thanks go to Dr. Kevin Kenow of the National Biological Service in LaCrosse, Wisconsin, for taking the time to patiently teach me the transmitter implant procedure. Financial support was provided by the Michigan Department of Natural Resources Wildlife Division through the Pittman-Robertson Act. The Ruffed Grouse Society also provided funding.

Valuable personal support and encouragement were provided by Carrie Thorvig. I cannot thank her enough for being there for me. Finally, my fellow graduate students in the Department of Fisheries and Wildlife deserve the rest of the credit. They made MSU life truly enjoyable.

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INTRODUCTION

The ruffed grouse (*Bonasa umbellus*) is the most widely distributed member of the Tetraoninae in North America, occurring in at least 47 states and provinces (Gullion 1977, Cade and Sousa 1985). It is considered the most important small game resource in 9 of those political districts. Between 1970 and 1974, 63% of ruffed grouse taken by hunters in North America were from Michigan, Minnesota, Ontario, and Wisconsin (Gullion 1977). Currently, about 125,000 hunters pursue ruffed grouse in Michigan each year (Winterstein et al. 1995:24). Although the ruffed grouse is most popular as a game bird, its presence in the forest is appreciated by hunters and non-hunters alike.

Much attention by wildlife researchers has been paid to the population dynamics of grouse. Understanding major periodic fluctuations in grouse abundance, known as the 10-year cycle, and the effect of hunting pressure have been of special interest (Criddle 1930, Bump et al. 1947, Palmer 1956, Marshall and Gullion 1965, Fischer and Keith 1974, Rusch et al. 1984, Stoll and Culbertson 1995). Fall-to-spring survival plays a key role in population fluctuations, but the importance of chick production and predispersal survival have also been recognized (Gullion 1970, Smyth and Boag 1984). Although much is known about the breeding and brooding behavior of grouse hens (Schladweiler

1965; Brander 1967; Barrett 1970; Maxson 1974*a*, *b*; Maxson 1978*a*, *b*), relatively little is known about the fate of their nests and chicks.

Nesting success, including the percentage of eggs that hatch, may depend on the quality of the nesting habitat. Various habitat components have been used to describe grouse nesting sites. Nests are generally adjacent to a solid object and are only a short distance from mature aspen trees and an opening (Bump et al. 1947; Maxson 1974*a*, 1978*a*; Gullion 1977). Relatively low densities of woody stems and herbaceous undergrowth are valuable features of the nest site as well (Bump et al. 1947, Gullion 1977, Maxson 1978*a*, Thompson et al. 1987). Nest sites may be further characterized by their distance from the nearest conifer tree and the aspect of the nest relative to other objects or the slope of the ground (Bump et al. 1947, Maxson 1974*a*, Thompson et al. 1987).

Some ruffed grouse are believed to make 2 nesting attempts in the same breeding season if their first nest is destroyed before incubation begins. The assumption of renesting is often based on evidence of a secondary peak in hatching that occurs a few weeks after the initial peak and usually involves notably smaller clutches (Cringan 1970, Porath and Vohs 1972, Maxson 1978*a*). The second nesting attempt of a marked hen has been documented in only 1 case (Barrett 1970).

A more complete understanding of grouse summer population dynamics has been limited by traditional methods of investigation. The ratio of the number of juveniles per adult male in the fall population is a common grouse recruitment index (Dorney and Kabat 1960). It is difficult, however, to quantify and account for the bias toward juveniles in sampling procedures such as trapping and hunter harvest. Porath and Vohs (1972) compared crude density from 15 July to crude density in early spring to measure grouse production. Also, brood flush counts have been used to measure grouse chick abundance (Ammann and Ryel 1963) and to estimate chick survival (Rusch and Keith 1971). Unfortunately, brood flush counts are dependent on several variable factors (Healy et al. 1980) and have proven to chronically underestimate brood size in grouse (Godfrey 1975, Kubisiak 1978). Apparent brood intermixing and the failure to account for total brood loss may also render brood size estimates based on flush counts unreliable.

This study was designed to provide opportunities for determining the rates and sources of predispersal mortality by marking individual grouse chicks with radio transmitters. A direct measurement of chick survival, as opposed to an indirect measurement or index, will lead to an improved year-round grouse population model. This study also was intended to document nesting parameters, such as clutch size and hatching dates, and nest site characteristics in northern Michigan for comparison with published data from other areas of the upper Midwest and Great Lakes region.

OBJECTIVES

The specific objectives of this study were to:

1. quantify habitat attributes related to grouse nest site selection,
2. determine grouse nesting success and the hatchability of grouse eggs, and
3. determine the survival of grouse chicks from hatching through fall dispersal.

STUDY SITES

This study was conducted during the spring and summer months of 1996 and 1997 in the northern portion of the lower peninsula of Michigan. The primary site was in the Maltby Hills region of the Huron National Forest (HNF). A second study site was located in the Pigeon River Country State Forest (PRCSF). The sites were divided into 2 areas--one that was closed to grouse and woodcock hunting and another, similarly-sized area that remained open to hunting under normal harvest regulations. Each of the 4 areas covered approximately 100 km^2 (Figure 1). The areas were designated as hunted or unhunted for purposes not related to this study (see Clark 1996, Gormley 1996).

The HNF site is found in parts of Alcona, Oscoda, and Ogemaw counties (44° 32' N lat., 83° 58' W long.). Stands of aspen (*Populus* spp.), sugar maple (*Acer saccarinum*), red pine (*Pinus resinosa*), white pine (*Pinus strobus*), white cedar (*Thuja occidentalis*), and oak (*Quercus* spp.) cover most of the area. The topography varies from nearly level to steep (up to 40% slopes) at elevations between 300 m and 430 m. Temperatures range from an average daily minimum in winter of -11 C to an average daily maximum in summer of 26 C. The area receives an average of 73 cm of precipitation each year,

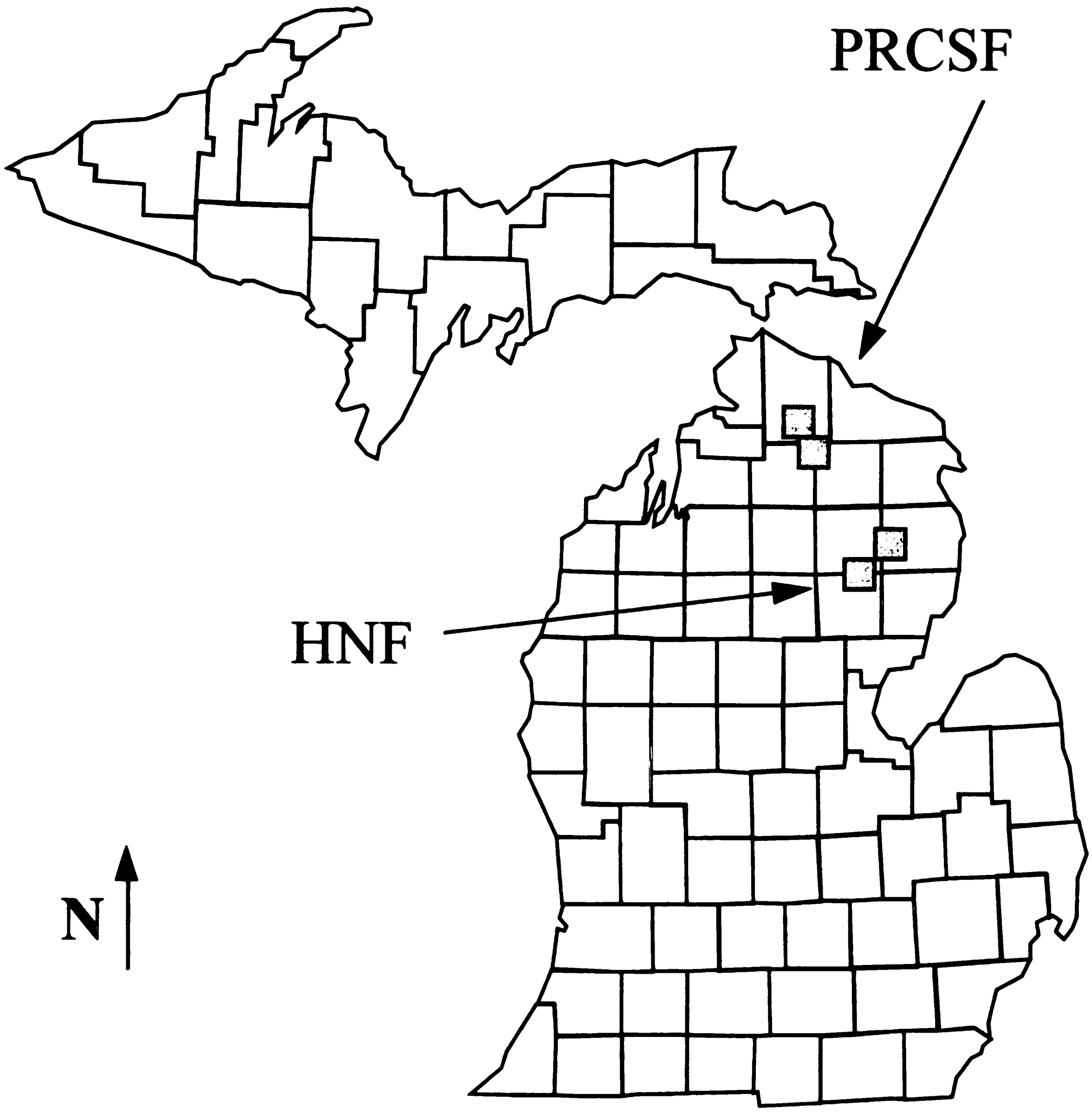

Figure 1. Map of Michigan counties indicating the location of the Huron National Forest (HNF) and Pigeon River Country State Forest (PRCSF) study sites.

about half of which occurs during the 120-day growing season (Johnson 1990). The months of April and May at the HNF site were approximately 3.3 degree-days warmer and received approximately 3.3 cm less precipitation in 1997 than in 1996 (Midwest. Climate Cent., unpubl. data).

The PRCSF site is found in parts of Cheboygan, Otsego, and Montmorency counties (45° 11' N lat., 84° 26' W long.). This site has vegetation and climate that are similar to those at the HNF site due to their proximity. Major differences between the 2 sites include the lack of large oak stands, level to only undulating topography, and a substantially shorter growing season of approximately 90 days at the PRCSF site (Tardy 1991). Detailed information about the forest structure, overstory vegetation, and grouse habitat at both study sites can be found in Gormley (1996).

METHODS

Locating Nests

Nests for this study were found by approaching radio-collared grouse that were located in the same place on 2 consecutive days during the nesting season. Therefore, it was essential to have hens with functioning radio-collars in the spring. In August and September of 1995 and 1996 grouse were captured using a modified version of the cloverleaf traps described by Dorney and Mattison (1956). Traps were checked every night between dusk and 3 hours after dark. Grouse in the traps were tagged with a uniquely numbered Michigan Department of Natural Resources leg band. They were aged as either hatch-year (<6 months old) or after-hatch-year (>12 months old) based on the shape and condition of the ninth and tenth primaries (Hale et al. 1954, Dorney and Kabat 1960, Godin 1960). The sex of each captured grouse was determined by the number of spots on each rump feather (Roussel and Ouellet 1975). Grouse that weighed >350 g and were uninjured were fitted with a bib-type radio transmitter (see Clark 1996, Gormley 1996 for a detailed description of fall trapping and handling procedures). All grouse were released about 10 m from the trap.

During the spring months of 1996 and 1997 attempts were made to replace the radio-collars on surviving female grouse because the battery in the transmitters was not expected to last more than 9 months. A nightlighting method was used early in the spring (Huempfner et al. 1975). However, if a hen initiated incubation before the replacement of her transmitter, attempts to recapture her were made during the day using a dip net.

In early May 1996, radio-collared grouse were monitored for drumming or nesting behavior, in case any errors had been made in determining sex the previous fall. This was not done in 1997 due to lack of success with this method. During both years all surviving grouse were monitored as if they were hens to avoid the possibility of not locating the nest of a radio-collared grouse simply because it was believed to be a male the previous fall. In addition, all radio-collared grouse for which no nest had been found, regardless of sex, were approached on foot and flushed during the week of 1 June in an attempt to locate nests.

Nest Sites

The age and dominant overstory vegetation type of forest stands containing located grouse nests were obtained from the Huron Shores and Mio district offices of the U.S. Forest Service for the HNF site and the PRCSF headquarters. Many other attributes of each nest site were analyzed after the nesting attempt was complete, and the hen was no longer occupying the nest. The spatial relationship between nests and any solid objects within 1 m were noted. The type and size of the objects were noted also, including the species if the object was a tree or snag. The orientation of nests from solid objects and the aspect of the ground slope were recorded as one of 8 general compass directions.

The density of live woody stems ≥ 1 m tall was measured in a 10- x 10-m plot centered on the nest with the corners being in the cardinal directions. Horizontal cover was quantified from a uniform height (0.5 m) and distance in front of the nest using a 1-m-tall profile board. Vertical cover at the nest, divided into ground cover (<1.5 m high) and canopy cover (>1.5 m high), was quantified by estimating the percent cover in a 1- x 1-m plot and using a spherical densiometer, respectively. Distances from the nest to the nearest opening, mature aspen tree (≥ 15 cm dbh), and conifer tree (≥ 1 m tall) were measured also. An opening was defined as an area having no live woody stems and no canopy cover for ≥ 5 m in one straight-line dimension.

Nest site characteristics were compared between years, study sites, and areas open and closed to hunting to determine the appropriateness of combining data within those categories. Then the combined data were used to compare the nest sites of first and second nests, yearling and adult hens, and successful and unsuccessful nests. Comparisons of the vegetation type and the type of object against which grouse nested were made using Chi-square tests. Comparisons of nest orientation and slope aspect were made using Fisher's exact tests (Sokal and Rohlf 1995:730-736). Preliminary analysis of nest site variables containing continuous data was conducted by assessing time series plots, using principal components analysis of the correlation matrix (PCA) (Morrison 1990:313-331), and a multivariate analysis of variance (MANOVA) (Morrison 1990:200-256). Then, in a few instances, pairwise comparisons were made with these data by performing individual *t*-tests or Kruskal-Wallis tests (Ott 1993:792-795). The significance of statistical tests described in this section was based on α = 0.05.

Nesting Parameters

Observed nest locations were marked in the field and on a map. Nests were revisited between 6 and 18 hours after being located to determine if egg laying was complete. This allowed for the prediction of a hatching date. Approximately 2 weeks after being located nests were observed to determine the final clutch size, if it was not known already. Nests were also approached if the hen was located off the nest or if the hen's radio signal indicated she was dead. This ensured that destroyed or abandoned nests were found as soon as possible. Destroyed nests were investigated to determine the type of predator that was responsible. All necessary precautions were taken to minimize disturbance when approaching a nest to make direct visual observations. Incubating hens were located daily using triangulation from up to 5 days prior to the predicted hatching date until the eggs hatched. These triangulations were made from a distance of 30-100 m from the nest. The initial brood size was determined by counting the number of eggs that did and did not hatch. Renesting attempts were monitored in the same manner as first nests.

Nest initiation was never observed, so the date had to be estimated using the earliest known point in the nesting sequence. A known point occurred if 2 different clutch sizes were observed, meaning that the nest was located during the egg-laying period, or if the eggs hatched. To estimate the initiation date from a known point during the egg-laying period 1.3 days for each egg were subtracted from the earliest date of clutch size determination (Maxson 1974*b*). To estimate the initiation date from the hatching date, 25 days for incubation and 1.3 days to lay each egg in the full clutch were subtracted from the hatching date. Initiation dates and hatching dates were recorded as the day of the year from 1 January. The Mayfield method was used to calculate nest survival rates (Mayfield 1961).

Nesting variables were compared between first and second nests, years, study sites, areas open and closed to grouse hunting, and yearling and adult hens. Two of the nesting variables, clutch size and nest initiation date, were also compared between successful and destroyed nests. Clutch sizes were compared using t tests. Egg hatchability was analyzed in 2 different ways. First, individual eggs were treated as the sampling units, and comparisons were made by testing for binomial proportions. Next, egg hatchability was analyzed using each nest as a sampling unit. Egg hatchability rates by nest were compared using the Wilcoxon rank sum test (Ott 1993:279-285). The Wilcoxon rank sum test was used also to compare nest initiation dates. The ratio of the difference in daily survival rates to the standard error of that difference (Z test) was used to compare Mayfield nest success rates (Johnson 1979).

Twenty-seven pairwise comparisons were required to analyze these data. A Bonferroni adjustment was made to control the experimentwise Type I error rate at 0.100 (Sokal and Rohlf 1995:240). Therefore, the significance of statistical tests described in this section was based on $\alpha = 0.004$.

Chick Survival

When broods were approximately 6 days old as many chicks as possible within a brood were collected by hand. Broods were approached on foot by a team of 2-5 people. Individual chicks were followed as the brood flushed. If fewer than 4 chicks were caught immediately, the team remained at the flush site and searched for up to 15 minutes. At the time of capture an attempt was made to estimate brood size for use in calculating a chick survival rate for the first week after hatching. Captured chicks were placed in a 4.7 L plastic pail lined with soft vegetation and transported to the vehicle (<0.8 km).

At the vehicle the chicks were transferred to a large cardboard box containing a hot water bottle at one end. The box was placed in the shade. Chicks were removed from the box one at a time to be processed. First, they were weighed to the nearest 0.5 g in a small plastic bag using a spring scale. Then they were positioned on a hot water bottle and held by an assistant during transmitter attachment. Crystal controlled two stage transmitters with a 12-week battery (model BD-2G, Holohil Systems, Ltd., Carp, Ont.) were used to individually mark chicks. Antennas were 17.5 cm long and had a total diameter of approximately 0.5 mm.

Two different transmitter attachment procedures were used. In the first procedure the transmitter was implanted just beneath the skin in the interscapular region (Korschgen et al. 1996). Stainless steel tubes were used to thread the antenna from an incision at the base of the neck to an exit site just above the tail. Then the antenna was used to pull the transmitter into place, and the neck incision was sutured closed with 1-2 mattress stitches. Implanted transmitters weighed 1.25 g and were 16- x 8- x 5-mm in size.

In the second attachment procedure transmitters were attached externally by sutures to the interscapular region. Transmitters attached by this method were fitted by the manufacturer with 2 tubes for the passage of suture material. Both tubes were positioned transversely on the ventral surface of the transmitter--one at the anterior end and one at the posterior end. External transmitters weighed 1.33 g and were slightly longer than the implanted transmitters (18 mm). Unwaxed dental floss was passed through each tube and then under approximately 5 mm of the chick's skin. The points where the 2 sutures were passed under the skin were slightly closer together than the tubes on the transmitter to allow for significant chick growth before the sutures would pull out (Figure 2). Livestock identification tag cement (Nasco, Fort Atkinson, Wis.) was applied to the ventral surface of the transmitter to secure it in place until the sutures healed. Each suture loop was tied with a square knot. A small amount of Krazy Glue was then applied to the knots.

In 1996, each transmitter attachment procedure was used an approximately equal number of times in each brood. In 1997, only the external suture technique was used. Radio-marked chicks were returned to their brood as soon as possible. The brood was flushed on the return visit so that the captured chicks could be placed directly with the unmarked chicks.

Figure 2. Schematic drawings of externally sutured transmitters.
A. Dorsal view of suture material being passed through the tubes and under the skin before the transmitter is flipped over into the proper position (dashed outline).
B. Lateral view of a 6- to 8-day-old chick with an external transmitter.
C. A 10-week-old chick showing that the suture points are allowed to grow apart longitudinally.

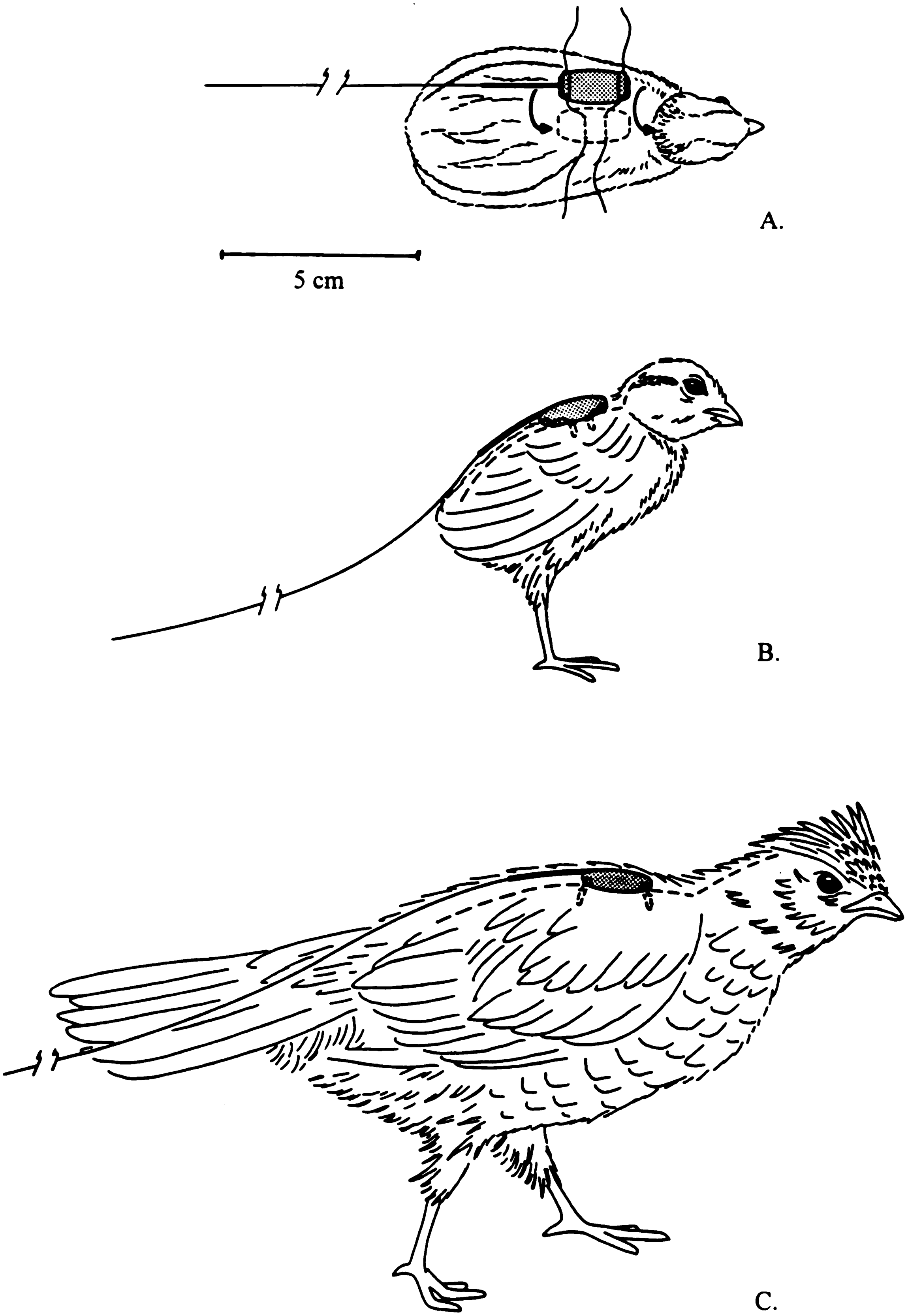

Figure 2. Schematic drawings of externally sutured transmitters.

Radio-marked chicks were located by triangulation 3-6 times per week. When a chick died its remains were collected and sent to a Department of Natural Resources laboratory. The results of a necropsy, the condition of the transmitter, and predator signs at the collection site were used to determine the cause of mortality. A chick was presumed to be dead if it was not with its hen. A marked chick in a brood whose hen did not have a functioning radio-collar was presumed to be dead if it was not with other marked brood mates or if it was in the same place where it was last located.

Survival probabilities for the radio-marked grouse chicks were calculated using the Kaplan-Meier Product Limit estimator. Survival probabilities were compared between years and between chicks with implanted transmitters and those with external transmitters using the log-rank test (Pollock et al. 1989).

All capturing, handling, and marking procedures were reviewed and approved by the All-University Committee on Animal Use and Care (AUF # 10/96-149-00).

Population Modeling

The nest survival rate, clutch size, egg hatchability, and chick survival rate were multiplied to give an estimate of grouse recruitment into the fall population relative to the number of hens that survived to nest the preceding spring. The grouse production data from this study were combined with the sex-specific fall-to-spring survival rates of grouse populations at the HNF and PRCSF sites from 1993 to 1997 (S. R. Winterstein, Mich. State Univ., unpubl. data) to develop a descriptive year-round population model for ruffed grouse in northern Michigan.

RESULTS

Locating Nests

Recapturing hens in the spring was conducted only at the HNF site. Four hens were successfully nightlighted in 1996, and 4 were recaptured on their nests in 1997. All hens at both sites probably attempted to nest. For both years combined at the HNF site nests were located for 22 of the 29 grouse that were identified as females at trapping the previous fall and that were alive after 1 May. Only 2 of the 7 for which no nest was located survived past 12 May, and they may have been misidentified at trapping or had their nests destroyed early in the egg-laying period before they could be located. Nests also were located for 4 of 10 grouse that survived to 1 May but whose sex was previously unknown. No nests, however, were located by flushing radio-collared grouse during the week of 1 June.

Nests were located for 10 of the 20 grouse hens at the PRCSF site that were alive as of 1 May. Nests may not have been located for the other half of the hens for several reasons. Five of the hens for which no nest was located died before 27 May and may have been killed before they were able to begin a nest. Others may have had their sex misidentified or had their nest destroyed before it could be located. Also, nest search effort was not as high and search methods varied slightly at the PRCSF site.

A total of 41 grouse nests were located during the study, 12 in 1996 and 29 in 1997. Two nests in 1996 and 4 in 1997 were renesting attempts. One of the first nests in 1997 did not belong to a radio-collared hen and is not included in the analysis of nesting and reproductive success parameters because only its fate was determinable. However, this nest is included in the nest site analysis below. A different nest is included in the analysis of nesting and reproductive parameters but not in the analysis of nest sites, so the total sample size in both data sets is 40 nests. First nests were 7-33 days old when they were located. The mean age of first nests at the time of location was 19 days, which corresponds to the second or third day of incubation. All second nests were located within 10 days of initiation.

Nest Sites

Nesting habitat varied greatly among hens. Forest stands containing marked grouse nests were of many types and were between 3 and 82 years old. Nest sites had stem densities between 1300 stems/ha and 30,200 stems/ha (median = 5900 stems/ha), had horizontal cover ranging from 5% to 100% at both 5 m (mean = 45%) and 15 m (median = 85%) from the nest, had ground cover between 15% and 100% (mean = 53%), and had canopy cover between 51% and 99% (median = 90%).

Grouse nests were located in 11 different types of dominant overstory vegetation. Due to the small sample of nests (n = 40) the types were combined into the following 3 major categories: 1) aspen (*Populus* spp.), which contained enough marked nests to warrant its own category, 2) other deciduous types, which includes northern hardwoods [mostly maple (*Acer* spp.)], oak (*Quercus* spp.)/hickory (*Carya* spp.), oak, and lowland brush, and 3) conifers, which includes jack pine (*Pinus banksiana*), jack pine/oak, red pine (*P. resinosa*), white pine (*P. strobus*), and swamp conifer. One of the original 11 vegetation types was grass/opening. The 1 nest located in that type was excluded as an outlier for this variable. The vegetation type classification was not indicative of the actual nest site, which was in an area containing trees and shrubs near the edge of the grass/opening. Similar numbers of nests were located in aspen and conifer types (approximately 35-40% of nests each), with only slightly fewer nests in other deciduous types (approximately 25% of nests). The proportion of nests in each category of overstory vegetation was similar between years, sites, areas open and closed to hunting, first and second nests, yearling and adult hens, and successful and unsuccessful nests (Table 1).

All nests were positioned against 1 of 5 objects--a live tree, a snag (standing dead tree), a stump, a log, or a branch laying on the ground. These objects were combined into the following 3 categories to reduce the degree to which the assumption of minimum expected values for the Chi-square test would be violated: 1) live trees, 2) other erect objects, which includes snags and stumps, and 3) objects laying on the ground, which includes logs and branches. Over 60% of nests were positioned against 1 or more live trees. The other nests were divided almost equally between the other 2 categories. The proportion of nests in each category was similar between years, sites, areas open and closed to hunting, first and second nests, yearling and adult hens, and successful and

Table 1. Dominant overstory vegetation type of ruffed grouse nesting sites in northern Michigan in 1996 and 1997.

	Aspen	Other deciduous[a]	Conifer[b]	X^2 Test statistic[c]	P-value[d]
Year					
1996	4	2	5	0.655	0.73
1997	9	7	8		
Site					
HNF	11	6	9	1.174	0.57
PRCSF	2	3	4		
Area					
open	9	6	7	0.734	0.70
closed	4	3	6		
Nesting attempt					
first	12	8	11	0.381	0.83
second	1	1	2		
Hen age[e]					
adult	6	3	6	0.307	0.86
yearling	6	5	7		
Nest fate					
successful	10	7	8	0.993	0.62
unsuccessful	3	2	5		

[a] This category includes maple, oak, oak/hickory, and lowland brush.
[b] This category includes jack pine/oak, jack pine, red pine, white pine, and swamp conifer.
[c] Test of independence between rows and columns. For example, there is no relationship between year and dominant overstory vegetation type.
[d] Significance based on $P < 0.05$.
[e] Two hens were of unknown age.

unsuccessful nests (Table 2). The only marginally significant result was that no second nests were positioned against an object laying on the ground, but there were only 6 nests in that sample, which makes interpretation tenuous.

The kind of tree or snag against which a grouse positioned its nest was identified at least to its genus. The 11 different kinds of trees and snags were combined into the same 3 categories that the dominant overstory vegetation types were. Aspens, as above, have their own category. The "other deciduous trees" category includes maple, oak, birch (*Betula* spp.), beech (*Fagus grandifolia*), and ironwood (*Carpinus caroliniana*). The "conifer" category includes balsam fir (*Abies balsamea*), jack pine, red pine, white pine, and white cedar (*Thuja occidentalis*). There were 10 nests associated with each of the 3 categories. Unexpectedly, tests indicated that years were significantly different (Table 3). Sites also were significantly different, but this was probably due to the differences in the proportions of various overstory vegetation types at the 2 study sites (Gormley 1996:24). The HNF is known to have a much higher proportion of coverage in aspen and other deciduous types, and the PRCSF is known to have a much higher proportion of conifer coverage. This difference in vegetation composition between sites contributes to the difference in object selection between years. In 1996 approximately equal numbers of nests were located at each site. In 1997, however, two-thirds of nests were at the HNF site, leading to many more nests positioned against aspen trees in that year. The study site difference also was evident in the number of nests located in the different dominant overstory vegetation categories, even though the comparison did not

Table 2. Objects against which ruffed grouse positioned their nests in northern Michigan in 1996 and 1997.

		Live tree	Snag or stump	Log or branch	X^2 Test statistic[a]	*P*-value[b]
Year						
	1996	10	1	1	3.180	0.22
	1997	15	6	7		
Site						
	HNF	17	4	7	1.765	0.43
	PRCSF	8	3	1		
Area						
	open	17	4	3	2.378	0.32
	closed	8	3	5		
Nesting attempt						
	first	22	4	8	5.849	0.055
	second	3	3	0		
Hen age[c]						
	adult	13	4	2	1.595	0.46
	yearling	11	3	5		
Nest fate						
	successful	20	4	4	3.265	0.21
	unsuccessful	5	3	4		

[a] Test of independence between rows and columns. For example, there is no relationship between year and type of object.
[b] Significance based on $P < 0.05$.
[c] Two hens were of unknown age.

Table 3. Species of live tree or snag against which ruffed grouse positioned their nests in northern Michigan in 1996 and 1997.

	Aspen	Other deciduous[a]	Conifer[b]	X^2 Test statistic[c]	P-value[d]
Year					
1996	0	5	6	8.900	0.013
1997	10	5	4		
Site					
HNF	9	8	4	6.667	0.038
PRCSF	1	2	6		
Area					
open	7	6	8	0.952	0.63
closed	3	4	2		
Nesting attempt					
first	9	10	7	4.038	0.146
second	1	0	3		
Hen age[e]					
adult	3	6	6	1.768	0.43
yearling	6	4	4		
Nest fate					
successful	7	9	7	1.491	0.48
unsuccessful	3	1	3		

[a] This category includes maple, oak, birch, beech, and ironwood.
[b] This category includes fir, jack pine, red pine, white pine and cedar.
[c] Test of independence between rows and columns. For example, there is a relationship between year and type of tree or snag.
[d] Significance based on $P < 0.05$.
[e] One hen was of unknown age.

reveal a statistically significant difference (Table 1). Over 40% of nests at the HNF site and only about 20% of nests at the PRCSF site were located in aspen stands.

When data were separated by study site the tree and snag species did not appear to differ by year at the PRCSF. Therefore, the comparisons of first and second nests, yearling and adult hens, and successful and unsuccessful nests were investigated within that site but with years combined (Table 4). There were no obvious differences. At the HNF site years still appeared to be different, so the last 3 comparisons were investigated within years at that site (Table 5). No obvious differences were apparent at the HNF site either.

The orientation of grouse nests relative to the object against which they were positioned did not differ by year, site, or areas open and closed to hunting (Fisher's exact test, $P > 0.7$ for all 3 comparisons). Nests were found in all 8 general compass directions. As expected, most first nests were found on the south and east sides of an object where they would receive direct sunlight in the morning and throughout much of the day (Figure 3). No second nests were found in these directions, but exposure to sunlight for heat would not be as important later in the spring when second nests are begun, and the difference between nesting attempts was not significant ($P = 0.082$). Nest orientation also was similar between yearling and adult hens (Figure 4, $P = 0.986$) and successful and unsuccessful nests (Figure 5, $P = 0.222$).

More than half of the nests were located on level ground. The aspect of the ground at nest sites that were located on a slope did not differ between years, sites, or areas open and closed to hunting (Fisher's exact test, $P > 0.5$ for all 3 comparisons).

Table 4. Species of live tree or snag against which ruffed grouse positioned their nests at the PRCSF study site in northern Michigan in 1996 and 1997.

	Aspen	Other deciduous[a]	Conifer[b]
Year			
1996	0	1	4
1997	1	1	2
Nesting attempt			
first	1	2	3
second	0	0	3
Hen age			
adult	1	2	5
yearling	0	0	1
Nest fate			
successful	0	2	5
unsuccessful	1	0	1

[a] This category includes only maple.
[b] This category includes fir, white pine, and cedar.

Table 5. Species of live tree or snag against which ruffed grouse positioned their nests at the HNF study site in northern Michigan in 1996 and 1997.

	Aspen	Other deciduous[a]	Conifer[b]
Year			
1996	0	4	2
1997	9	4	2
1996			
Nesting attempt			
first	0	4	2
second	0	0	0
Hen age			
adult	0	3	1
yearling	0	1	1
Nest fate			
successful	0	3	1
unsuccessful	0	1	1
1997			
Nesting attempt			
first	8	4	2
second	1	0	0
Hen age[c]			
adult	2	1	0
yearling	6	3	2
Nest fate			
successful	7	4	1
unsuccessful	2	0	1

[a] This category includes maple, oak, birch, beech, and ironwood.
[b] This category includes jack pine and red pine.
[c] One hen was of unknown age.

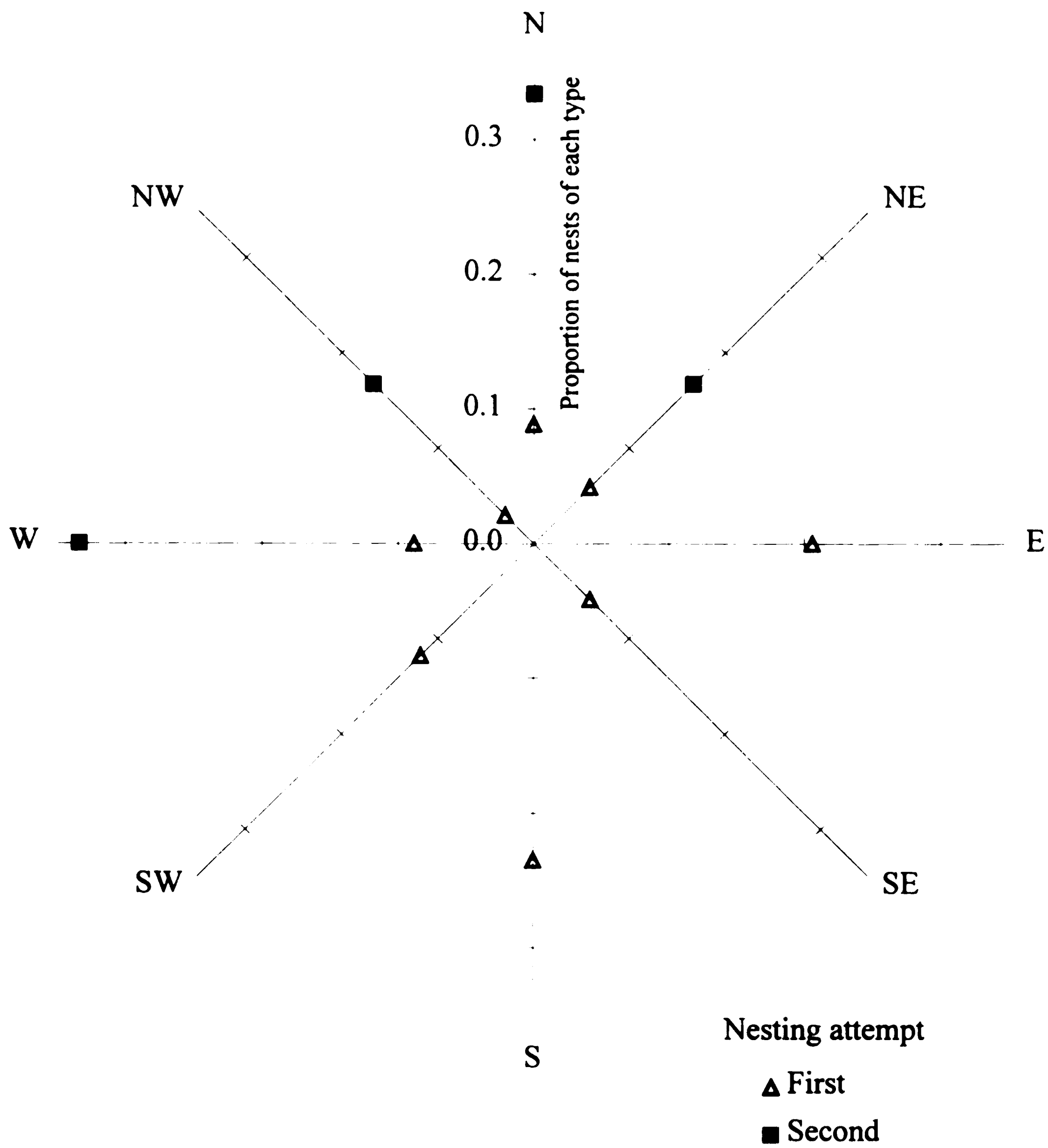

Figure 3. Proportion, by nesting attempt, of ruffed grouse nests oriented in each of 8 general compass directions from a solid object. Proportions may not sum to 1 because orientation was not recorded for 4 nests that were positioned under an object. $P = 0.082$ for Fisher's exact test.

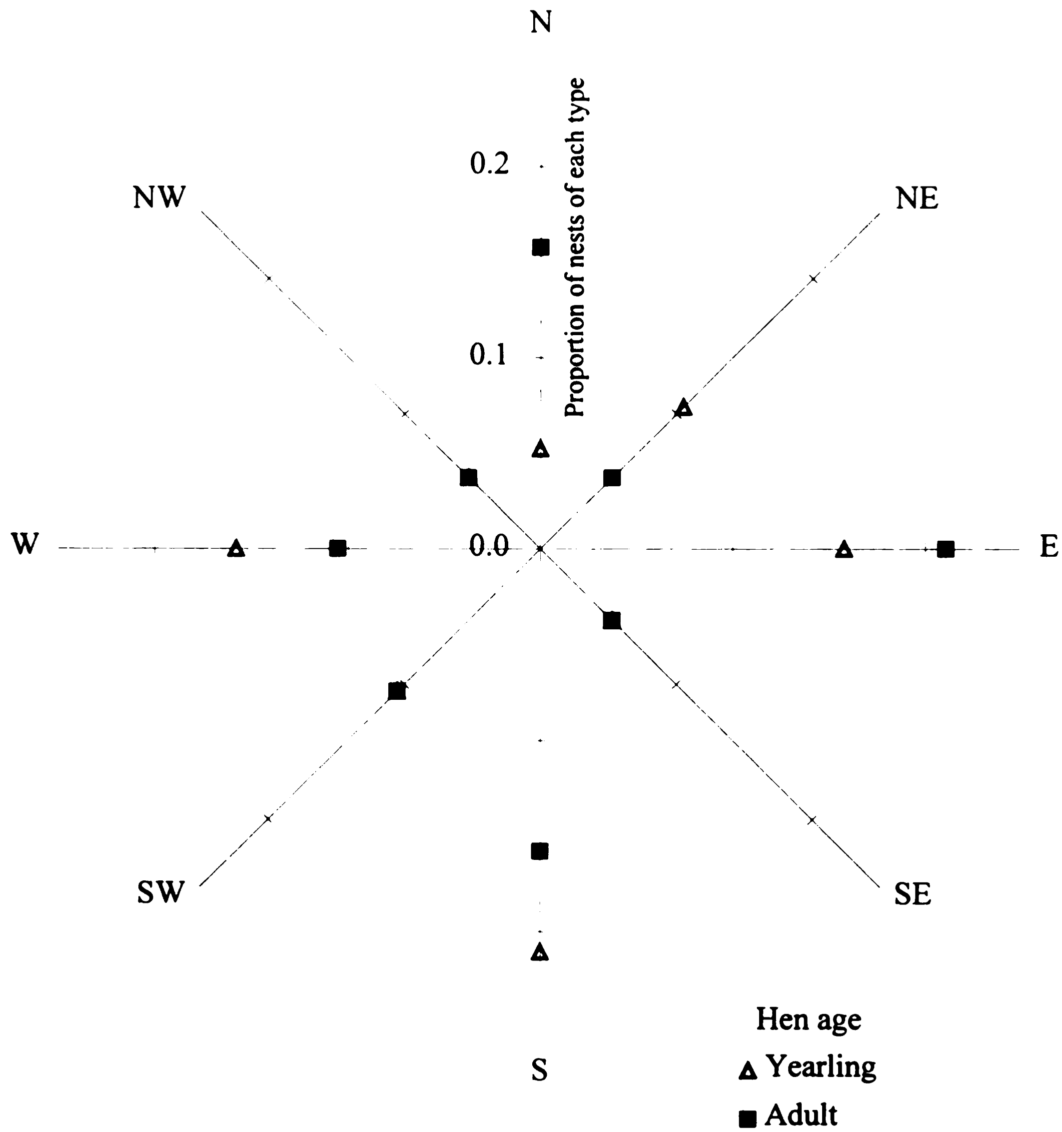

Figure 4. Proportion, by hen age, of ruffed grouse nests oriented in each of 8 general compass directions from a solid object. Proportions may not sum to 1 because orientation was not recorded for 4 nests that were positioned under an object. $P = 0.986$ for Fisher's exact test.

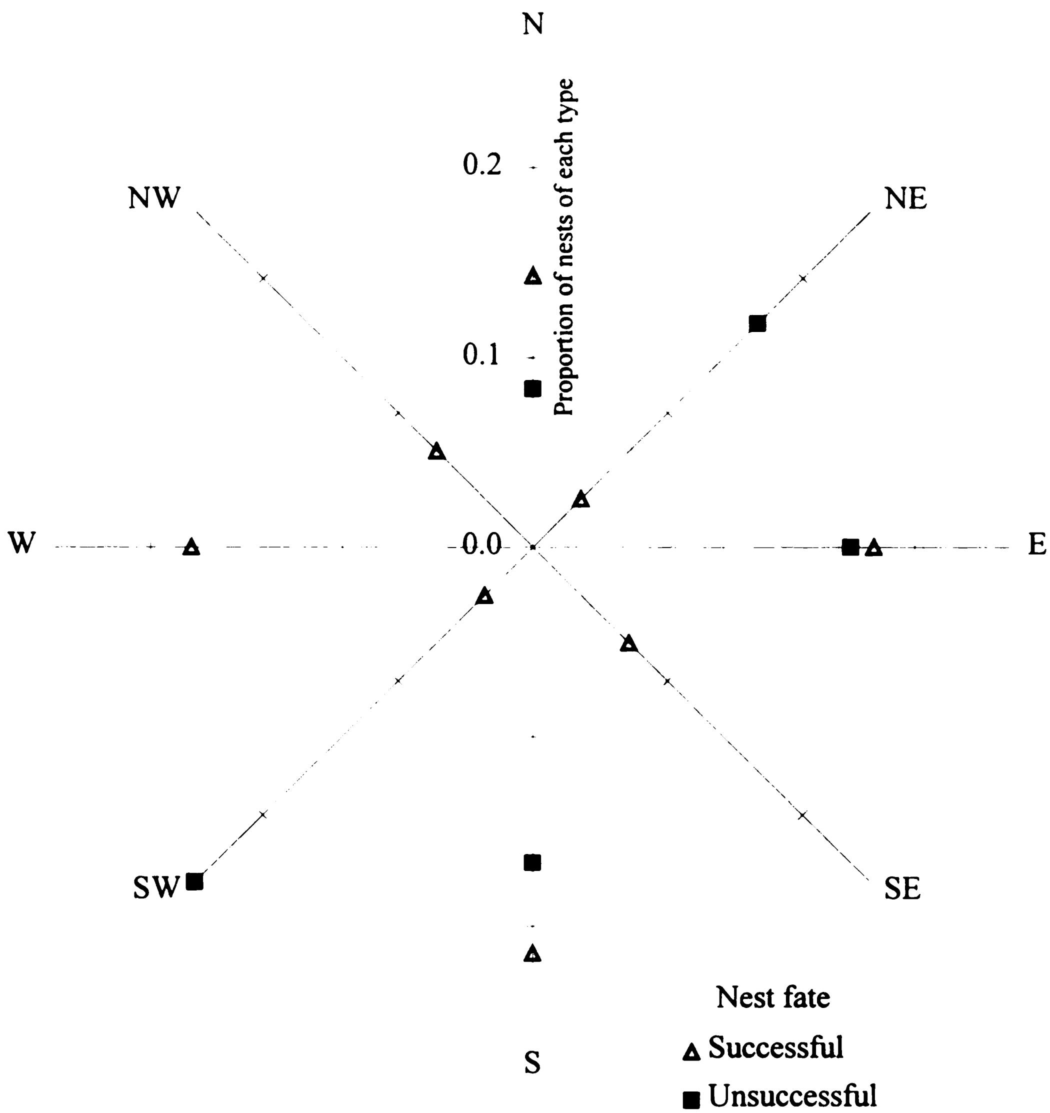

Figure 5. Proportion, by nest fate, of ruffed grouse nests oriented in each of 8 general compass directions from a solid object. Proportions may not sum to 1 because orientation was not recorded for 4 nests that were positioned under an object. $P = 0.222$ for Fisher's exact test.

Most nests on slopes had at least some southerly or easterly exposure, and more were sloped to the south-east than any other direction. First and second nests (Figure 6, $P > 0.999$), nests of yearling and adult hens (Figure 7, $P = 0.558$), and successful and unsuccessful nests (Figure 8, $P = 0.094$) also did not differ according to slope aspect.

No trends over time were detected in most of the nest site variables containing continuous data. However, the values for horizontal and ground cover were markedly higher at the PRCSF site in 1996 than in 1997 or in either year at the HNF site (variances were still similar). This difference was not sufficiently large to elicit a significant overall year effect in the MANOVA for the PRCSF site, but the cause is obvious. The values of these variables change dramatically as herbaceous vegetation continues to emerge in the summer. Nest site data at the HNF study site were collected between 11 June and 15 June in 1996 and between 11 June and 3 July in 1997. Data were collected on nest sites at the PRCSF study site on 7 July 1997, which was similar to the timing of vegetation sampling at the HNF site, but not until 7 August in 1996.

Only 28 nests could be used for principal components analysis when the stand age and diameter of nest tree variables were included because they contained missing data, so PCA also was run once without using the diameter variable and once without using either the stand age or diameter variables. When the diameter of the nest tree was included it did not appear to contribute much to the variability in the significant principal components, so emphasis was placed on the latter 2 PCA trials. They yielded similar results. Starting with 9 and 8 variables, the 2 trials accounted for 83% and 87% of the variability in the first 5 principal components, respectively. Inspection of the eigen

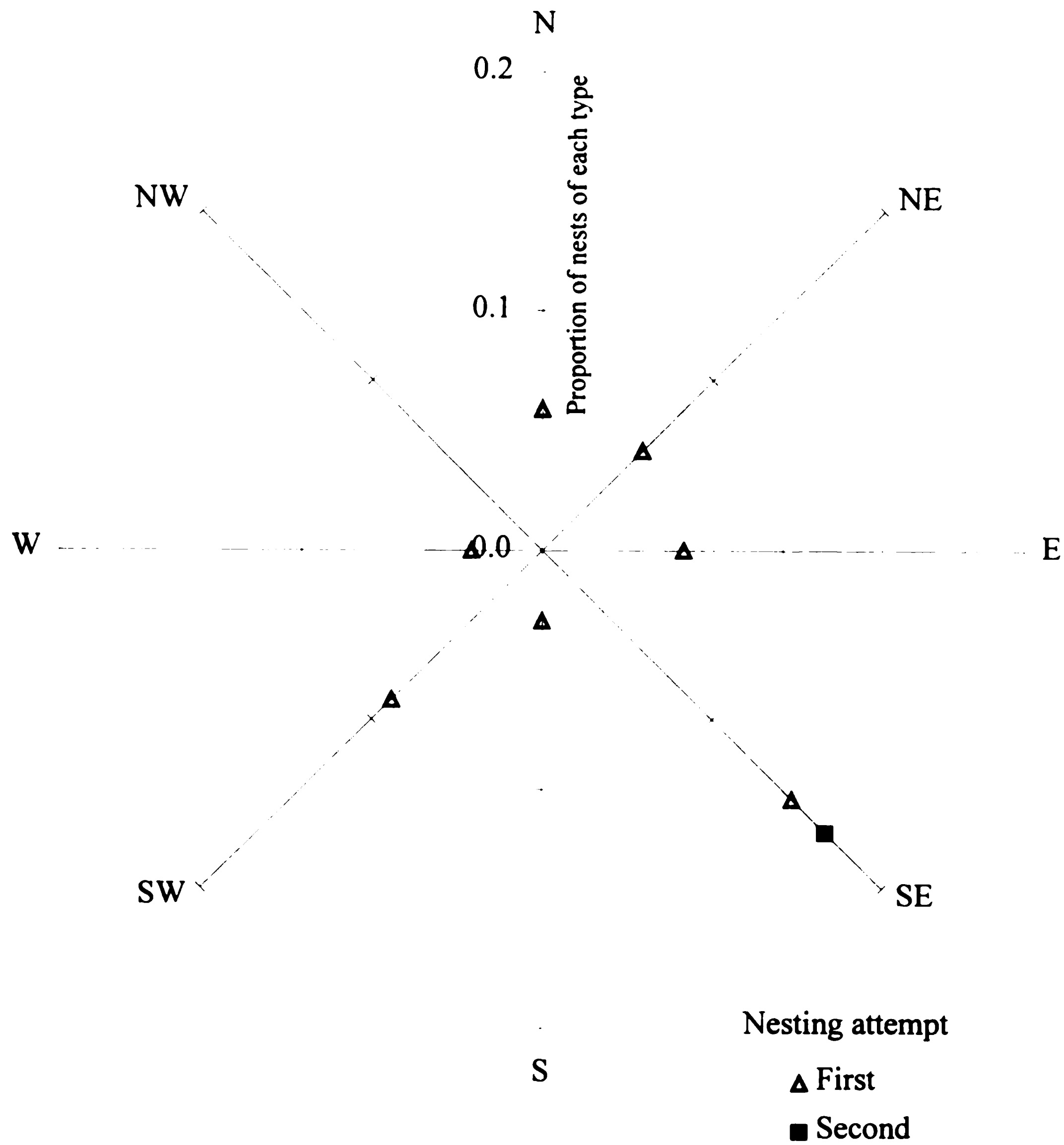

Figure 6. Proportion, by nesting attempt, of ruffed grouse nest sites with a slope aspect in each of 8 general compass directions. Proportions do not sum to 1 because slope aspect was not recorded for 23 nests that were on level ground. $P > 0.999$ for Fisher's exact test.

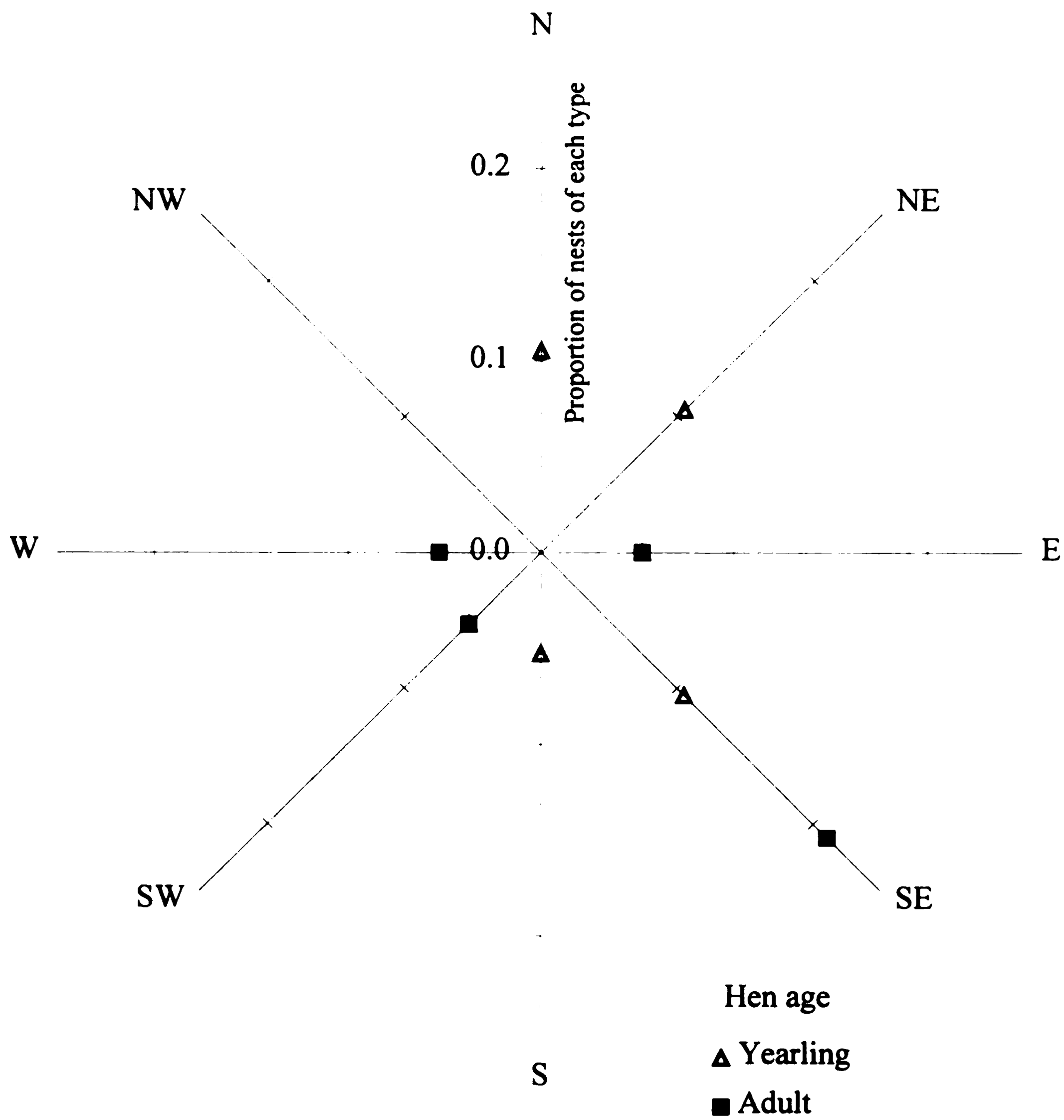

Figure 7. Proportion, by hen age, of ruffed grouse nest sites with a slope aspect in each of 8 general compass directions. Proportions do not sum to 1 because slope aspect was not recorded for 23 nests that were on level ground. $P = 0.558$ for Fisher's exact test.

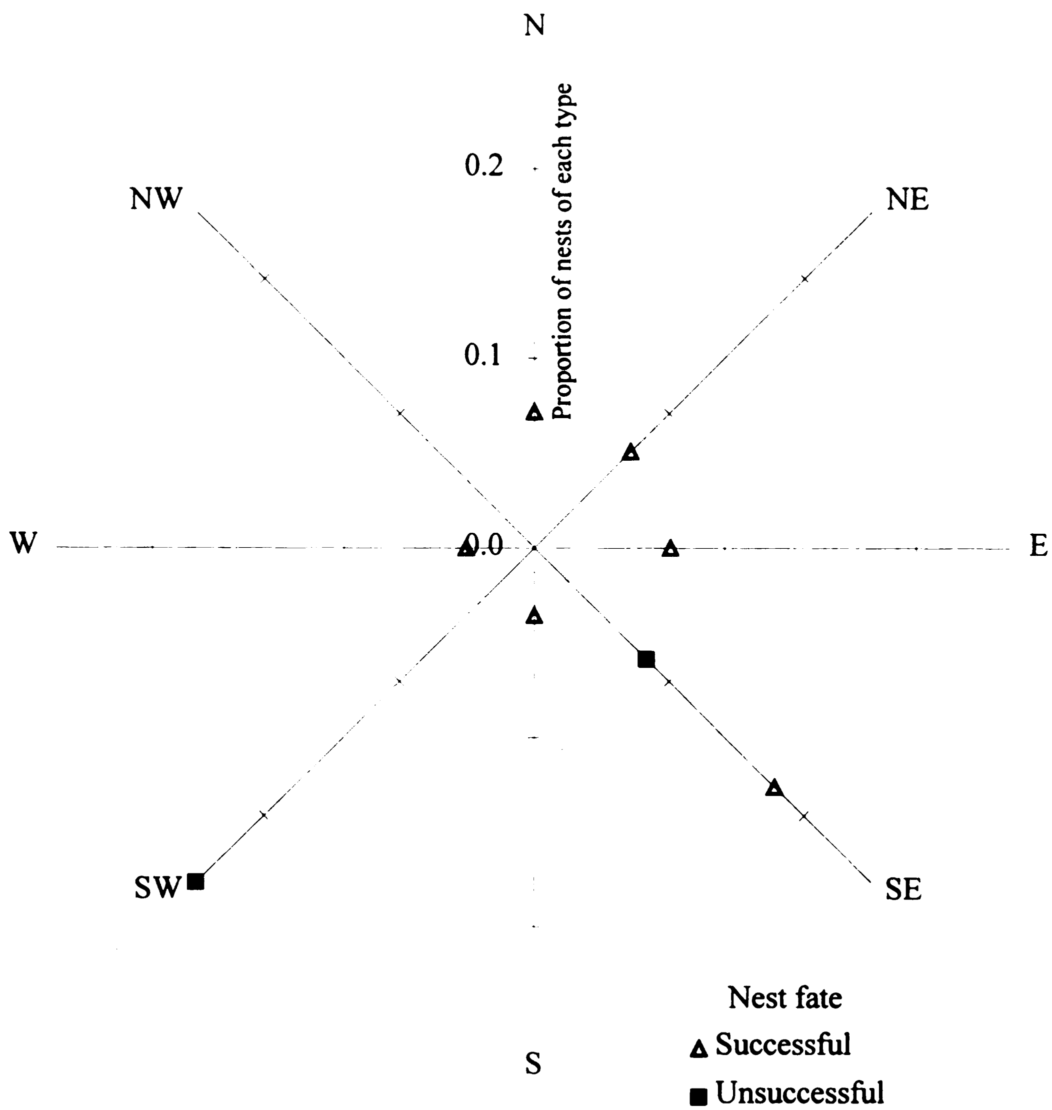

Figure 8. Proportion, by nest fate, of ruffed grouse nest sites with a slope aspect in each of 8 general compass directions. Proportions do not sum to 1 because slope aspect was not recorded for 23 nests that were on level ground. $P = 0.094$ for Fisher's exact test.

vectors indicated that stand age, horizontal cover from 15 m, and canopy cover contributed most to the variability in the data, and horizontal cover from 5 m never contributed much variability to the first 5 dimensions. Biplots were constructed from the first 3 dimensions, which accounted for >60% of the variability. When the independent variables (year, site, area, nesting attempt, hen age, nest fate) were used as data labels no groupings were evident, indicating that the pairwise groupings were not separated along the dimensions of highest variability.

Multivariate analysis of variance also is sensitive to missing data, so 2 separate MANOVAs were used to analyze the stand age and diameter of nest tree variables and the other 8 variables containing continuous data. The data were fit to a model containing the independent variables of year, site, and area (open vs. closed to hunting), as well as the 2-way interactions among them. There were not enough degrees of freedom to test for a 3-way interaction. The overall effect of the site x area interaction was significant ($P = 0.0282$). There were not enough degrees of freedom to test for any interactions among year, site, and area when running a MANOVA for the stand age and diameter of nest tree variables, but the overall effect of both site and area were significant (both $P < 0.003$). Visual inspection of graphs and individual ANOVAs indicated that 2- or 3-way interactions were present in nearly all of the variables.

Next, an additional set of MANOVAs were conducted for the HNF and PRCSF sites separately. This was done to reduce the site x area interaction to an overall area effect and for the intuitive reason that there were known differences in stand-level vegetation between the HNF and PRCSF sites (Gormley 1996). In general, most forest stands at the PRCSF site were older and contained larger trees at lower densities than the stands at the HNF site (Table 6). A better developed understory in the more mature forest at the PRCSF site also resulted in more horizontal and ground cover there. The MANOVA models contained the variables year and area as main effects, and there were sufficient degrees of freedom to test for a year x area interaction at the PRCSF site only. None of these overall effects were significant at the HNF site (all $P > 0.135$) or the PRCSF site (all $P > 0.650$). Therefore, continuous nest site data were combined between years and areas within sites.

These combined data were used in MANOVAs for the model containing the independent variables of nesting attempt, hen age, and nest fate. Within sites there were not sufficient degrees of freedom to test for interactions. The overall main effects were not significant at either site. However, a few of the individual ANOVAs indicated possible differences between a few groups. The subsequent pairwise tests for these possible differences were all significant. At the HNF site first nests appeared to be much closer to the nearest aspen tree (Kruskal-Wallis test, $P < 0.001$), but there was only one second nest in the comparison (Table 6). At the PRCSF site second nests were positioned against larger trees than first nests (t-test, $P = 0.0311$), and unsuccessful nests were located much closer to the nearest aspen tree than successful nests (Kruskal-Wallis test, $P < 0.001$).

Table 6. Median nest site characteristics of ruffed grouse in northern Michigan in 1996 and 1997.

	n	Stand age (yrs)[a]	Diameter of nest tree (cm)[bc]	Stems /ha	Horizontal cover from from 5 m (%)[c]	Horizontal cover from 15 m (%)	Ground cover (%)[c]	Canopy cover (%)	Distance to nearest opening (m)	Distance to nearest aspen (m)	Distance to nearest conifer (m)
Site											
HNF	28	24	10	7150	41	83	49	91	18	6	5
PRCSF	12	71	20	3500	55	90	60	88	12	22	1
HNF											
Nesting attempt											
first	27	24	10	6700	39	80	50	91	18	6[d]	5
second	1	18	10	8000	75	90	35	88	7	160[d]	6
Hen age[e]											
adult	8	46	10	8050	36	85	55	91	18	6	2
yearling	18	22	10	6350	41	80	45	90	15	24	12
Nest fate											
successful	20	23	9	7650	41	90	50	91	16	6	6
unsuccessful	8	47	13	5150	39	73	47	92	20	19	5

Table 6 (cont'd)

	n	Stand age (yrs)[a]	Diameter of nest tree (cm)[bc]	Stems /ha	Horizontal cover from from 5 m (%)[c]	Horizontal cover from 15 m (%)	Ground cover (%)[c]	Canopy cover (%)	Distance to nearest opening (m)	Distance to nearest aspen (m)	Distance to nearest conifer (m)
PRCSF											
Nesting attempt											
first	7	71	12[f]	4600	47	85	58	87	35	72	1
second	5	53	27[f]	2700	65	95	63	89	4	9	0
Hen age											
adult	11	71	17	3800	56	95	60	87	13	35	1
yearling	1		35	1300	40	45	55	97	3	6	0
Nest fate											
successful	8	81	19	4400	59	98	61	91	9	76[g]	1
unsuccessful	4	64	21	3150	46	80	59	87	23	3[g]	2

[a] Stand age was determined for only 25 nest sites in the HNF and 5 nest sites in the PRCSF.
[b] Only 21 nests in the HNF and 9 nests in the PRCSF were positioned against a tree or snag. This characteristic does not apply to the other nests.
[c] Means are given for diameter of nest tree, horizontal cover from 5 m, and ground cover. Values for all other characteristics are medians.
[d] Significantly different using a Kruskal-Wallis test ($P < 0.001$).
[e] Two hens at the HNF site were of unknown age.
[f] Significantly different using a *t*-test ($P = 0.0311$).
[g] Significantly different using a Kruskal-Wallis test ($P < 0.001$).

Nesting Parameters

The date of initiation was determined for 33 nests (Figure 9). It ranged from 26 April to 4 June. There was no overlap between the initiation dates of first and second nests. The median date of first nest initiation was 1 May (day 121 from 1 January). This was similar between years, sites, areas open and closed to hunting, yearling and adult hens, and successful and destroyed nests. However, nesting did appear to begin about 4 days earlier in 1997 than in 1996, but this difference was not statistically significant (P = 0.038; experimentwise $\alpha = 0.10$, with Bonferroni adjustment individual significant α = 0.004) (Table 7). When the 4 first nests from the PRCSF site for which the initiation date was known were removed the difference in initiation dates between years at the HNF site was only about 2 days. The possible earlier nesting in 1997 may be attributable to the warmer, drier weather during the month of April in that year (see Study Sites section above).

Ten first nests were destroyed. Two of these nests were not observed. They were presumed to have been destroyed before they could be located because the only nests located for 2 of the hens were initiated relatively late and had relatively small clutch sizes and were, therefore, presumed to be second nesting attempts.

Of the 5 yearling hens that survived the destruction of their first nest, 2 made a second attempt at nesting that same year. All 4 of the adult hens that could have renested did. One of the 10 hens was of unknown age.

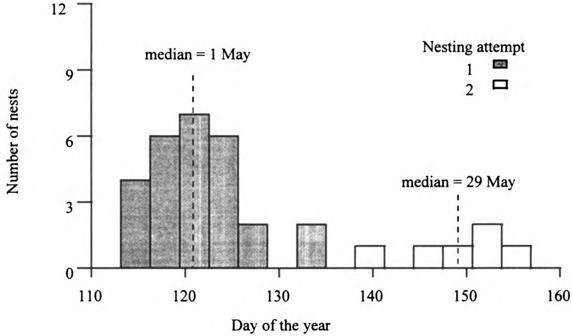

Figure 9. Distribution of ruffed grouse nest initiation dates in northern Michigan in 1996 and 1997.

Table 7. Nest initiation dates (day of the year from 1 January) of ruffed grouse in northern Michigan in 1996 and 1997. Day 121 is 1 May.

	First nesting attempts				Second nesting attempts[a]	
	n	median	test statistic[b]	*P*-value[c]	*n*	median
Year						
1996	9	122.0	166	0.04	2	147.5
1997	18	118.5			4	149.5
Site						
HNF	23	121.0	52	>>0.10	1	148.0
PRCSF	4	119.5			5	151.0
Area						
open	20	120.5	106	>>0.10	1	155.0
closed	7	123.0			5	148.0
Nesting attempt						
first	27	121.0	183	<<0.01		
second					6	149.5
Hen age[d]						
adult	12	121.0	0.78[e]	0.44	4	151.0
yearling	14	120.5			2	146.5
Nest fate[f]						
successful	23	120.0	41	0.10	5	148.0
destroyed	2	124.5			1	151.0

[a] No statistical comparisons were made between groups of second nests.
[b] Wilcoxon rank sum T.
[c] Significance based on $P < 0.004$ (see Methods for Bonferroni adjustment).
[d] One hen was of unknown age.
[e] A z statistic was used because both $n_i > 10$.
[f] Two abandoned nests were not included.

Three of the hens that could have renested but did not had been incubating for ≥6, ≥10, and 20 days, respectively, when their first nest was destroyed. The fourth hen had not begun incubating her first nest. Two of the hens that did attempt a second nest also had not begun incubation when their first nest was destroyed. The same is likely true for the 2 presumed first nests. The other 2 hens that attempted second nests had been incubating for ≥9 and ≥13 days, respectively, when their first nest was destroyed.

The date of first nest destruction for hens that subsequently attempted a second nest ranged from 22 May to 28 May but was perhaps as early as 15-20 May for the presumed first nests. Two of the hens that did not attempt a second had their nests destroyed during the same time period. The other 2 nests for which there were no second attempts were destroyed during the first week of June. Second nests were initiated 3 to 6 days after the destruction of the first nest. The median date of second nest initiation was 29 May (day 149) (Figure 9).

Hatching dates of the 28 successful nests ranged from 4 June to 3 July (Figure 10, Table 8). There was no overlap in hatching dates between first and second nests. The median hatching date for first nests was 10 June (day 161). The median hatching date for second nests was 1 July (day 182). Hatching dates were similar between years, sites, areas open and closed to hunting, and yearling and adult hens. They were not compared statistically because they were highly correlated with initiation dates ($r = 0.98$), for which there was only one significant difference (first versus second nests), and they were more similar between categories than initiation dates. Conducting formal statistical tests was unnecessary and only would have inflated the overall Type I error rate.

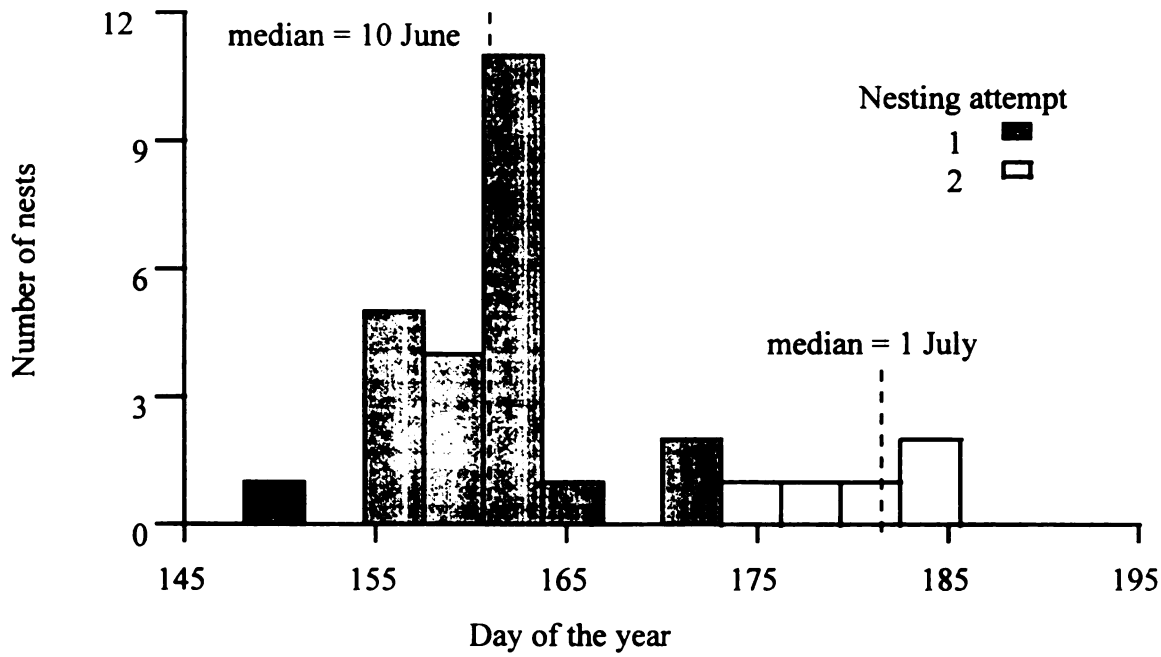

Figure 10. Distribution of ruffed grouse hatching dates in northern Michigan in 1996 and 1997.

Table 8. Hatching dates (day of the year from 1 January) of ruffed grouse in northern Michigan in 1996 and 1997. Day 161 is 10 June.

	First nesting attempts		Second nesting attempts	
	n	median	*n*	median
Year				
1996	6	162.0	2	179.5
1997	17	161.0	3	182.0
Site				
HNF	19	161.0	1	182.0
PRCSF	4	161.0	4	180.5
Area				
open	16	161.0	1	185.0
closed	7	161.0	4	179.5
Nesting attempt				
first	23	161.0		
second			5	182.0
Hen age				
adult	12	162.0	3	184.0
yearling	11	160.0	2	179.5

The duration of the incubation period was determined for 5 nests. Three first nests had incubation times of 24, 25, and 27 days for clutches of 13, 13, and 14 eggs, respectively. The 2 second nests had incubation times of 21 and 26 days for 8 and 7 egg clutches, respectively.

Full clutch size was determined for 30 first nests (Table 9). The mean was 12.7 eggs. This was significantly higher than the mean of 7.3 eggs in the 6 second nests. The 95% confidence interval for the difference in clutch size between first and second nests is 4.0 to 6.8 eggs. Clutch sizes were similar between years, study sites, open and closed areas, yearling and adult hens, and successful and destroyed nests.

Egg hatchability also was significantly higher in first nests than second nests (Table 10). Whereas 95.9% of the eggs in the 23 successful first nests hatched, only 83.3% of the eggs in the 5 successful second nests hatched ($P < 0.002$). This difference in hatchability is also evident when nests are used as the sampling units, although at a lower level of significance ($P = 0.020$). The proportion of successful nests experiencing 100% egg hatchability was 83% for first nests and 20% for second nests. Egg hatchability was significantly higher in open areas than closed areas when eggs were the sampling units ($P < 0.003$) but not when nests were the sampling units ($P > 0.1$). The significant difference between areas is due entirely to a first nest in the closed area of the HNF site in which only 5 of 13 eggs hatched. This nest was only 2 m from a forest road that experienced heavy traffic from logging trucks during the 2 days prior to hatching. All of the eggs from the other 6 successful first nests in closed areas hatched, which explains the insignificant result when nests were analyzed. If the disturbed nest were

Table 9. Clutch size of ruffed grouse nests in northern Michigan in 1996 and 1997.

	First nesting attempts					Second nesting attempts[a]		
	n	mean	SE[b]	*t* statistic	*P*-value[c]	*n*	mean	SE[b]
Year								
1996	9	12.33	0.41	-0.90	0.378	2	8.00	0.00
1997	21	12.90	0.38			4	7.00	0.41
Site								
HNF	23	12.70	0.25	-0.23	0.819	1	7.00	
PRCSF	7	12.86	0.99			5	7.40	0.40
Area								
open	20	12.85	0.33	-0.56	0.580	1	8.00	
closed	10	12.50	0.58			5	7.20	0.37
Nesting attempt								
first	30	12.73	0.29	8.01	<0.001			
second						6	7.33	0.33
Hen age[d]								
adult	14	12.86	0.44	-0.31	0.758	4	7.75	0.25
yearling	15	12.67	0.42			2	6.50	0.50
Nest fate[e]								
successful	23	12.87	0.28	-0.82	0.420	5	7.20	0.37
destroyed	5	12.20	1.28			1	8.00	

[a] No statistical comparisons were made between groups of second nests.
[b] Standard error.
[c] Significance based on $P < 0.004$ (see Methods for Bonferroni adjustment).
[d] One hen was of unknown age.
[e] Two abandoned nests were not included.

Table 10. Egg hatchability (%) of ruffed grouse in northern Michigan in 1996 and 1997. Numbers are for first nests unless otherwise indicated.

	Egg as sampling unit				Nest as sampling unit			
	n	hatch-ability	*z* statistic[a]	*P*-value[b]	*n*	median	test statistic[c]	*P*-value[b]
Year								
1996	76	97.4	0.73	0.466	6	100.0	64	>>0.100
1997	220	95.5			17	100.0		
Site								
HNF	245	95.1	1.62	0.105	19	100.0	56	>0.100
PRCSF	51	100.0			4	100.0		
Area								
open	212	98.1	3.00	0.003	16	100.0	85	>>0.100
closed	84	90.5			7	100.0		
Nesting attempt								
first	296	95.9	3.16	<0.002	23	100.0	35	0.020
second	36	83.3			5	87.5		
Hen age								
adult	158	97.5	1.42	0.156	12	100.0	0.84[d]	0.401
yearling	138	94.2			11	100.0		

[a] Test for binomial proportions.
[b] Significance based on $P < 0.004$ (see Methods for Bonferroni adjustment).
[c] Wilcoxon rank sum T.
[d] A z statistic was used because both $n_i > 10$.

removed as an outlier, the difference in hatchability between first and second nests would increase. Egg hatchability was similar between years, study sites, and yearling and adult hens.

Each of the 40 nests in this study was under observation for 2 to 28 days. The median was 21 days, and the total was 753 nest-days for the 40 nests. Twenty-eight nests were successful, 9 were destroyed, and 3 were abandoned when the hen was killed during the egg-laying or incubation periods. The success rate of first nests was 47.8% (Table 11). This was lower than the 80.3% success rate of second nests only because it took longer to lay the larger clutch of first nests. The 1.2% difference in daily survival rate between first and second nests was not statistically significant ($P = 0.184$). However, first nests surviving to hatch were at risk an average of 40.1 days, and second nests were at risk for only 32.6 days. For all other comparisons of nest survival parameters, second nests were included in the summation of the number of nest-days and the number of nests that failed (see Mayfield 1961). However, only the mean time from initiation to completion (hatching) of first nests was used to calculate nest survival rates for the entire nesting period. Nest success rates and number of days at risk were similar between years, study sites, open and closed areas, and yearling and adult hens (Table 11).

Chick Survival

In 1996, 26 transmitters--13 implants and 13 externals--were placed on chicks from 8 different broods. Radio-marked chicks were eventually divided among 9 broods because of brood mixing, but the number of marked chicks per brood remained between 1 and 6. Eleven of the chicks marked in 1996 were at the PRCSF site, and 6 of them

Table 11. Mayfield nest survival rates of ruffed grouse in northern Michigan in 1996 and 1997.

		n	Failed nests	Observed nest-days	Daily survival (%)	Test statistic[a]	*P*-value[b]	Period survival (%)[c]
Year								
	1996	12	4	226	98.23	0.24	0.810	48.84
	1997	28	8	527	98.48			54.08
Site								
	HNF	27	7	523	98.66	0.77	0.444	58.19
	PRCSF	13	5	230	97.83			41.46
Area								
	open	23	6	448	98.66	0.65	0.516	58.19
	closed	17	6	305	98.03			45.00
Nesting attempt								
	first	34	11	604	98.18	1.33	0.184	47.83
	second	6	1	149	99.33			80.29[d]
Hen age[e]								
	adult	19	4	367	98.91	0.92	0.358	64.42
	yearling	20	7	364	98.08			45.93

[a] *Z* test; ratio of the difference in daily survival rate to its standard error.
[b] Significance based on $P < 0.004$ (see Methods for Bonferroni adjustment).
[c] Nest survival for the entire nesting period based on a mean completion time (from nest initiation to hatching) of 40.13 days for first nests.
[d] Based on a mean completion time of 32.60 days for second nests.
[e] One hen was of unknown age.

were from a second nesting attempt. In 1997, 50 transmitters were placed on chicks from 12 different broods, with 1 to 6 marked chicks per brood. These transmitters were all of the external type and were attached to chicks only at the HNF site.

At the time of capture chicks were 5 to 10 days old ($\bar{x}$ = 6.4 days) and weighed 16.0 to 43.0 g ($\bar{x}$ = 23.1 g). It was not possible to estimate chick survival from hatching to the time of transmitter attachment in either year because there were still too many chicks in the broods at the time of capture to be counted accurately.

Chicks that died within 5 days of transmitter attachment were not included in the calculation of survival rates because their deaths were presumed to be related to the stress of capture and handling. Four chicks were not included in survival calculations in 1996 because they died within 3 days of transmitter attachment. The survival rate from 14 June through 7 September 1996, was 31.1% (Figure 11). At the end of that period 6 chicks were still alive, and 2 were censored (Table 12). Ten of the 14 chick mortalities occurred in the first half of the predispersal period.

Chicks with external transmitters had a higher survival rate than those with implants, 42% versus 13% (Figure 12). This result, however, is not considered significant (log rank test, P = 0.5). One implanted transmitter and 2 external ones remained attached and functional into October 1996.

Only 2 marked chicks were excluded from the 1997 sample for survival calculations because they died within 5 days of transmitter attachment. The trend toward higher chick mortality early in the summer is more evident in 1997 than it was in 1996 (Figure 11). Only 1 chick died after 25 July in 1997. Chick survival from 9 June to 7

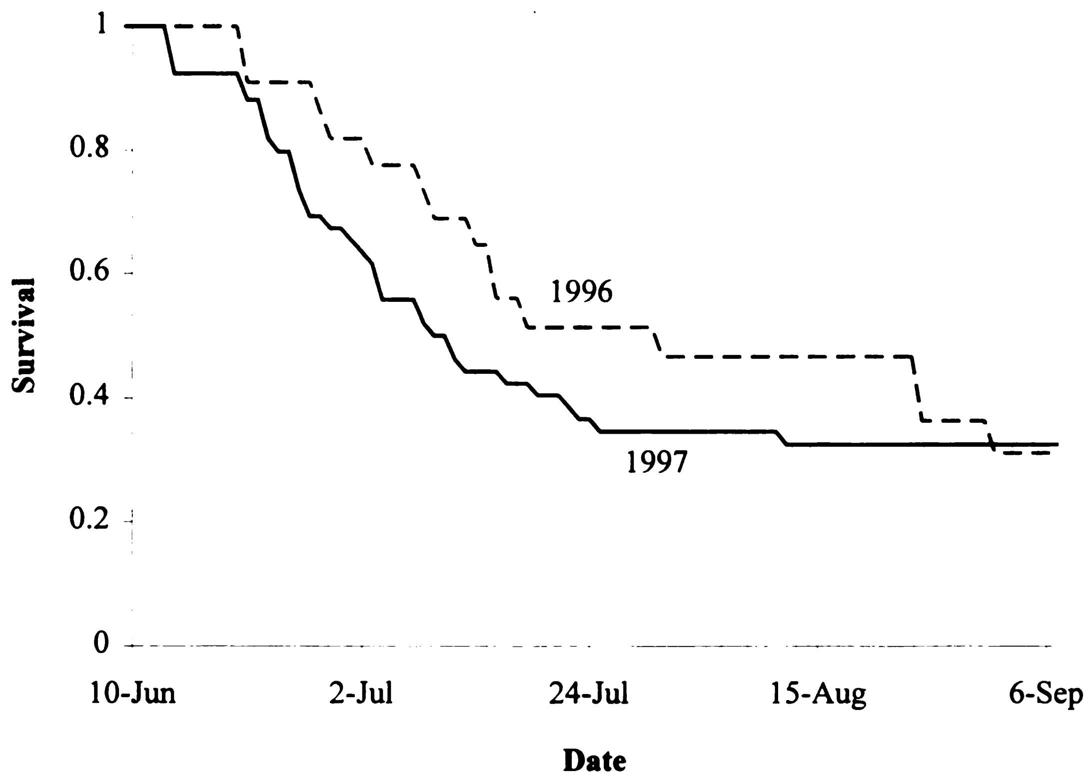

Figure 11. Survival of ruffed grouse chicks in northern Michigan. Survival rate to 7 September was 31.1% in 1996 and 32.5% in 1997. The 2 curves are statistically similar (log rank test, $P = 0.75$).

Table 12. Ending status and sources of mortality of ruffed grouse chicks in northern Michigan during the summers of 1996 and 1997.

	14 June-7 Sept., 1996		9 June-7 Sept., 1997	
Alive	6		8	
Censored	2		9[a]	
Dead	14		31	
avian predation		4 (29%)		16 (52%)
mammalian predation		2 (14%)		4 (13%)
exposure		0 (0%)		1 (3%)
no diagnosis		8 (57%)		10 (32%)
Not included[b]	4		2	
Number of transmitters placed in use	26		50	

[a] Four of the censorings in 1997 occurred after 2 September.
[b] Chicks that died within 5 days of transmitter attachment. Mortality presumed to be related to capture stress, so the chicks were not included in survival calculations.

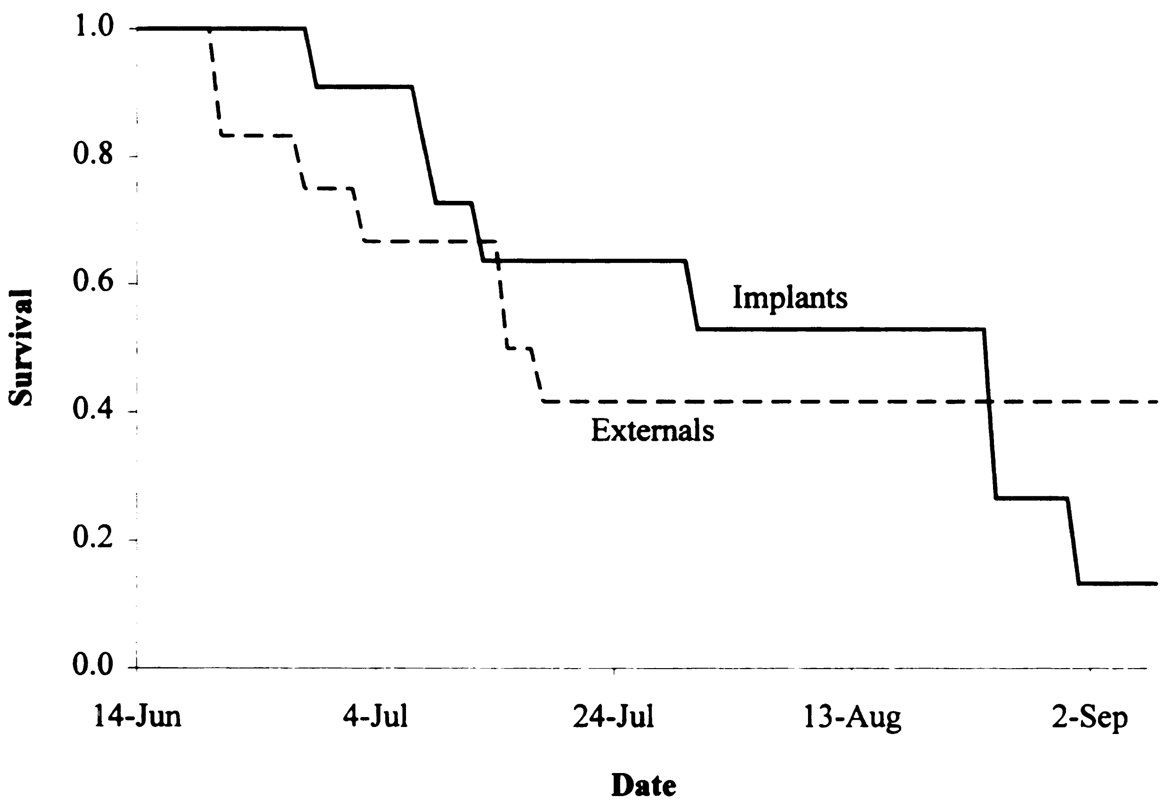

Figure 12. Survival of ruffed grouse chicks with different methods of transmitter attachment in northern Michigan in 1996. Each curve represents 11 chicks. Survival rate to 7 September was 41.7% for chicks with external transmitters and 13.3% for chicks with implants. The 2 curves are statistically similar (log rank test, $P = 0.50$).

September 1997, was 32.5%. At the end of that period 8 chicks were still alive, and 9 were censored (Table 12). Four of the censorings occurred during the first week of September, which is when the transmitter batteries were expected to begin failing and the fall dispersal period begins.

The cause of death was determined for fewer than half of the mortalities in 1996 (Table 12). Twice as many deaths were due to avian predators than mammalian predators. Sixteen of the 31 mortalities in 1997 were known to have been caused by avian predators, and 4 were due to mammalian predators. No source of mortality ("no diagnosis" in Table 12) could be determined for many of the chicks in both years because there were no remains to collect except a transmitter with no distinguishing holes, dents, or scratch marks that may be left by a predator.

On 2 occasions in 1996 and 3 in 1997, 2 marked chicks from the same brood died on the same day. Their remains were located 10-150 m apart, and in 2 of the cases it was determined that both chicks died from the same source, avian predators. These results indicate that the survival times were probably not independent within these pairs of chicks. Although this violates an assumption of the Kaplan-Meier procedure, it affects only the variance of the survival estimates, not the value of the estimates themselves.

Five marked chicks were involved in brood mixing before mid-August during the study. Three marked chicks in 1996 left their original broods within 2 days of capture. One of these was located back with its original brood 2 months later, but only for a day. The 2 marked chicks that mixed with other broods in 1997 left their original broods after

37 and 58 days, respectively. One of these also returned to its original brood for a day approximately 1 month after it had left.

Two radio-collared hens with broods containing marked chicks died during the study. One was killed by an avian predator on 23 August 1997. Her 2 marked chicks remained together for at least 4 days, and both survived until at least 3 September when they were censored, probably because of transmitter battery failure. The other hen was killed on 13 July 1997, when her chicks were 38-39 days old. She had 3 marked chicks, and at least 7 others flushed with them when the brood was approached to collect the hen's remains. One of the marked chicks remained with its marked brood mates for 4 days and was killed by an avian predator on 25 July. It is uncertain whether the chick was alone during its last week. The other 2 marked chicks remained together for 5 days. One of them was with at least 1 other unmarked chick for up to another week. It was censored on 23 August. The third marked chick was flushed alone on 25 July. On 25 August it was located with a marked chick from the other brood whose hen was killed. The next day it was censored.

Population Modeling

Grouse chick production from first and second nests were estimated separately because of the significant differences between first and second nests in survival rates during the entire nesting period, clutch size, and egg hatchability. For every 100 hens that begin nesting, the first nest survival rate indicates that approximately 48 will have a successful first nest (Table 13). Hatching a mean of 12.2 chicks, those 48 hens will

Table 13. Relative ruffed grouse chick production for every 100 females that survived to begin nesting in northern Michigan in 1996 and 1997.

	First nests	Second nests	Sum
Number of hens attempting to nest	100.0	24.1	100.0[a]
Number of hens with a successful nest[b]	47.8	19.4	67.2
Initial brood size[c]	12.2	6.1	
Total number of hatchlings[d]	583.2	118.3	701.5
Number of chicks surviving to dispersal[e]	186.6	37.9	224.5

[a] Although approximately 124 *nests* are attempted, hens attempting a second nest are also represented in the number of hens that attempted a first nest, so the total number of individuals is still 100 *hens*.
[b] Product of the number of hens attempting a nest and the nest survival rate.
[c] Product of clutch size and egg hatchability.
[d] Product of the number of hens with a successful nest and the initial brood size.
[e] Product of the total number of hatchlings and the predispersal survival rate (~0.32).

produce 583 hatchlings. Initial brood size is the product of clutch size and egg hatchability. Of the 52 hens whose first nest was unsuccessful at least 46% (6 of 13 hens in this study), or 24, will be expected to attempt a second nest. This proportion may be slightly higher because up to 4 of the hens in this study that did not appear to attempt a second nest may have but abandoned it or had it destroyed before it was found. One-hundred-eighteen chicks will be produced by the 19.4 successful (the product of the number of hens attempting a nest and the nest survival rate) second nests, which hatch an average of approximately 6.1 chicks each. An estimated 32% of the 702 hatchlings from both first and second nests will survive to disperse. This results in approximately 225 juvenile grouse recruited into the fall population in early September for each 100 hens that begin nesting. Given that some hens that begin nesting do not survive until fall and assuming a juvenile sex ratio of 1:1 at dispersal, there would be approximately 200 female grouse in the early fall population.

Adult female grouse at the HNF and PRCSF study sites had fall-to-spring survival rates of 0.61, 0.32, and 0.38 in 1994-95, 1995-96, and 1996-97, respectively. Juvenile females had fall-to-spring survival rates of 0.53, 0.17, and 0.47 during the same years, respectively. All females combined had fall-to-spring survival rates ≥ 0.45 during 2 of the 3 years. Supporting material for the results of fall-to-spring survival are provided in Appendix A.

Given the fall recruitment estimate from this study, the female segment of the grouse population would need to have at least a 50% survival rate during the fall-to-spring period to sustain a steady grouse population. Female survival rates do reach that level, although not consistently. The mean fall-to-spring survival estimate for females from 1994 to 1997 was 0.42. At this level of survival recruitment into the fall population would need to be at least 2.38 (instead of the observed 2.25) juveniles per spring hen to sustain a steady grouse population.

DISCUSSION

Nest Sites

Within areas of suitable nesting habitat it appears that individual grouse hens probably select nest sites nearly at random. Suitable nesting habitat can be described only in general terms. Nearly all dominant overstory vegetation types are used. Some researchers have found a strong preference for hardwoods--less than 5% of nests in studies by Bump et al. (1947:127-128) and Maxson (1978*a*) were located in conifer cover types--but more than a third of the nests in this study were located in conifer stands.

The age of a forest stand also appears to be less important than the actual cover it provides. Gullion (1977) reported that aspen stands between 25 and 30 years old provide preferred nesting habitat because stem densities are below 4900 stems/ha and the closed canopy prevents the growth of dense understory vegetation, which supposedly aid the incubating hen in detecting predators. By comparison, none of the 13 aspen stands that contained nests during the current study were 25-30 years old. Nine were younger, and 4 were older. Bump et al. (1947:127-128) reported that half of the nests in their 13-year study were in "second growth" forests, and the other half were split nearly equally between "young" and "mature" forests. The hens in my study also nested in forest stands of nearly all seral stages.

Although stem density results from a study of nest sites in an oak/hickory forest (Thompson et al. 1987) agree with Gullion's (1977) prediction, fewer than half of the nests sites in this study were in areas of <4900 stems/ha. This is probably due to the definition of a stem that was used. The density of live woody stems >1 m tall is usually much higher than the density of larger (for example >2-3 cm in diameter) erect woody stems in the same area. Stem density measurements that include only the relatively large stems are better descriptors of the quality of grouse nesting habitat because they indicate the degree of forest thinning to which Gullion (1977) was referring. On the other hand, the inclusion of the numerous, relatively small stems in determining stem density, as was done in this study using a definition by Cade and Sousa (1985), seems to provide only a redundant measure of understory cover.

No previous studies quantifying the amount of cover around ruffed grouse nest sites have been found in the literature, and only Bump et al. (1947:128) have given a qualitative description. They found 40% of their nests in areas with "sparse undergrowth," 46% in areas with "medium undergrowth," and 13% in areas with "dense undergrowth." The apparent nest success rate in their study was not affected by the density of undergrowth. Maxson (1978*b*), however, did find a higher apparent nest success rate in mixed hardwoods, where a thick covering of ferns emerged during the incubation period, than in oak stands where it did not. The amount of cover, quantified by several visual obstruction methods, did not appear to affect nest survival in the current study. Bracken ferns (*Pteridium aquilinum aquilinum*) were not present when grouse hens selected their nesting site, but they did provide much of the horizontal cover and ground cover at most of the nest sites subsequent to the nesting season and presumably during the later stages of incubation.

Ruffed grouse hens do prefer to position their nest against a solid object. Most nests are at the base of trees, but other large portions of dead or dying trees that are on the ground are utilized also. Although all nests in this study were positioned against a large object, it does not appear that objects are necessary because several nests found by Bump et al. (1947:130) and Maxson (1978*a*) were not associated with any kind of object. For those nests against trees, the size of the tree does not appear to be important. Maxson (1978*a*) reported that nest trees in his study were 5-29 cm in diameter. Nest trees in this study were 1-35 cm in diameter. Also, at the PRCSF renesting hens selected trees that averaged 15 cm larger in diameter than trees near first nests (Table 6). No meaningful explanation can be found for this result. One may not be necessary considering that the comparison is based on a small sample of only 4 first nests and 4 second nests, and no such difference was found at the HNF site. There is no strong evidence in this study to suggest that groups of grouse hens have preferences with respect to nest tree size.

This study found that there were more first nests on the south and east sides of the object against which the nests were positioned than there were on the north and west sides (Figure 3). More than half of the nests were on flat ground, but of the ones positioned on a slope there was a slightly higher proportion facing south-east than any other direction, and none of the slopes were facing north-west (Figures 6-8). Maxson (1978*a*) found a slight preference for the south and south-west side of nesting objects and slope aspect. Thompson et al. (1987) reported finding 12 of 13 grouse nests on south- or west-facing slopes. Considered together, these results suggest that ruffed grouse hens may have a weak preference for at least some southerly exposure of their nests. The mild significance of this suggestion is minimized by the fact that all 4 cardinal directions were selected in abundance in this study and others (Bump et al. 1947:130, Maxson 1978*a*).

The final attempt in this study to describe grouse nesting sites was to quantify the distance to other objects of possible importance to grouse hens, namely, the nearest conifer tree, open area, and mature aspen tree. Conifer trees have been considered detrimental to the quality of fall-to-spring habitat for ruffed grouse (Gullion 1977, Cade and Sousa 1985). Hammill and Moran (1986), however, assert that conifer cover can be a positive attribute of the habitat if both cover and long-range visibility are provided in the stand. No speculation on the advantages or disadvantages of conifer trees in grouse nesting habitat has been found in the literature. The results of this study agree with those reported by Bump et al. (1947:132) (Table 6). Although approximately half of the nests in each of the 2 studies were within 6 m of the nearest conifer tree, 21% of the nests in the earlier study were >150 m from the nearest conifer tree, and nests in the current study were up to 285 m from the nearest conifer tree. The distance to the nearest conifer tree does not appear to negatively impact nesting success, and Bump et al. (1947:132) explain that, conversely, conifers do not seem to be a necessary element of the nesting habitat, either.

The proximity of grouse nests to a forest opening is thought to be related to brood habitat preferences rather than any significant benefit for the hen during the nesting period. The distances to the nearest opening determined in this study are remarkably similar to the results from 2 other studies (Table 6). Nearly 50% of all nests were within 10 m of an opening (Maxson 1978*a*), and 75% were within 30 m (Bump et al. 1947:132-134). As expected, none of these studies revealed any effect of distance to the nearest opening on nest survival.

The buds of mature aspen trees are known to be an important food resource for ruffed grouse throughout the winter. Schladweiler (1968) found that grouse hens continue to rely almost solely upon mature aspen trees (12-23 cm dbh) for food during the nesting period, not for the buds but for the emerging leaves. Therefore, it may be expected that the proximity to mature aspen trees would be important in the selection of a nesting site. However, the nesting hens in a study by Maxson (1978*b*) rarely fed on the nearest aspen trees. The nearest aspen trees were within 80 m (median = 29 m), but incubating hens traveled up to 185 m (median = 75 m) to the aspen trees in which they fed. The 2 hens Schladweiler (1968) observed utilized aspen trees up to 90 m away from their nest. It appears that as long as there are aspen feeding sites within some threshold range of probably not less than 100 m, the distance of the nearest mature aspen tree is of little importance. The distances to the nearest mature aspen tree in my study are similar to those reported by others, so the statistical differences I found [1 second nest at the HNF site and the successful nests at the PRCSF site were much farther from the nearest mature aspen tree than first nests and unsuccessful nests at the respective study sites (Table 6)] are not likely to be ecologically significant.

Nesting Parameters

Ruffed grouse nest initiation and hatching dates are thought to be highly dependent on latitude, with the nesting season beginning earlier in the more southern portions of its range. Fisher (1939), working in 3 areas of Michigan within 100 km of the HNF and PRCSF study sites, found the mean hatching date for all but 1 nest to be 9 June. The excluded nest hatched on 8 July. These dates match the median first nest hatching date of 10 June and the last second nest hatching date of 3 July in this study (Figure 10, Table 8). At approximately the same latitude in Minnesota hatching dates averaged 4 June and 8 June in 2 different years (Maxson 1978*a*). In latitudes just south of the HNF and PRCSF study sites--the state of New York, most of southern Ontario, and central Wisconsin--hatching peaked near 1 June (Bump et al. 1947:284, Cringan 1970, Kubisiak 1978). Still further south--southernmost Ontario and northeastern Iowa--hatching peaked during the last week in May (Cringan 1970, Porath and Vohs 1972). Porath and Vohs (1972) reported a peak in the hatching of second nests 3 weeks after the peak for first nests. The difference between the median hatching dates of first and second nests in the current study was exactly 21 days, which suggests that the timing of second nests relative to first nests may be consistent regardless of latitude.

Although it is uncertain exactly why it appears that some hens whose first nest is destroyed attempt a second nest and some do not, the date of first nest destruction surely is one factor. If a hen's first nest is destroyed in early May when it contains only a few eggs, it is likely she would attempt a second nest. This is because the risk and metabolic costs of both nesting attempts combined is not much higher than for 1 complete first nest. Also, the possible benefit of producing chicks is much higher than producing no chicks if she were to not attempt a second nest, especially considering that ruffed grouse hens rarely survive through more than 2 breeding seasons. If, on the other hand, a hen's first nest were destroyed in early June, she would not be expected to renest because the chicks resulting from her second nesting attempt probably would not have sufficient time to mature before winter, and her additional reproductive effort would be wasted. For hens whose first nest is destroyed in mid- to late May, however, the probability that they would attempt a second nest must depend on other factors.

The stage of the nesting sequence when the first nest is destroyed may be one such factor. It has been considered unlikely that grouse hens would attempt a second nest if they had begun incubation of their first nest before it was destroyed. In a study by Maxson (1978*a*) none of the 6 hens whose first nest was destroyed during incubation renested. Also, the only positively documented occurrence of a grouse's second nesting attempt was of a hen whose first nest was destroyed before incubation began (Barrett 1970). The current study, however, has documented the nesting sequence of 4 ruffed grouse hens throughout their first and second nesting attempts in the same year. Two of the hens were at least 9 days into incubation before their first nest was destroyed. Also, 1 hen did not attempt a second nest even though she had not yet begun incubation of her first nest when it was destroyed. Therefore, the stage of the nesting sequence may not be as important as previously thought.

The data in this study suggest that the age of the hen may influence whether or not a second nest is attempted. Whereas 2 yearling hens renested and 3 did not, all 4 of the adult hens that had the opportunity to renest did. These data are few, however, and do not warrant any strong conclusion. No other reference to the effect of hen age on likelihood of attempting a second nest was found in the literature.

The remaining discussion in this section on nesting parameters will deal with the strictly quantitative variables that influence nesting productivity. Clutch size, nest survival, and egg hatchability, along with the proportion of hens that attempt first and second nests, determine the maximum possible increase in the grouse population each year.

The mean clutch size of first nests in this study was 12.7 eggs (Table 9). It is higher than the means of 11.5 and 11.9 eggs in "early nests" found in other studies (Bump et al. 1947:361, Cringan 1970) and the means of 10.6-12.5 eggs reported by those who did not distinguish between first and second nests (Fallis and Hope 1950, Fisher 1939, Leopold 1933:362, Maxson 1978*a*, Rusch and Keith 1971). The mean clutch size of second nests in this study was 7.3 eggs. It is lower than the means of 7.5 and 8.5 eggs in "late nests" reported by Bump et al. (1947:361) and Cringan (1970). The differences between the results for clutch size from this study and others probably is due to the lack of or imprecise classification of first and second nests in earlier studies.

Bump et al. (1947:359-360) suggested that yearling hens may produce smaller clutches than older hens. This conclusion was based on captive grouse and 1 wild hen that was observed with clutches of 10, 13, and 12 eggs when she was 1, 2, and 5 years old, respectively. Maxson (1978*a*), however, reported that there was no difference in average clutch size between adults and yearlings. Mean clutch sizes in this study also were not significantly different by hen age, but the mean for yearlings was slightly smaller than for adults for both first and second nests (Table 9). An inspection of nesting records for individual grouse hens lends more support to the conclusion above. Four hens had their full first nest clutch size observed for at least 2 years. In 3 cases the first year of observation was 1995, so 3 years of data were possible. Hen #140 laid 12 eggs as a yearling and 13 eggs each of the next 2 years. Hen #143 also laid 12 eggs as a yearling and 13 eggs the next year. The age of hen #173 was not known when she was first captured, and she laid clutches of 11, 14 and 12 eggs in 3 successive years. Hen #6024 was at least 2 and 3 years old when she laid clutches of 12 eggs each. It appears that perhaps the variability in clutch size among hens prevents the detection of a difference in clutch size according to hen age that is apparent within individual hens.

Nest success rates for ruffed grouse have been reported only as the percentage of nests found that hatched chicks, which ranged from 59% to 86% (Bump et al. 1947:312, Maxson 1978*a*, Rusch and Keith 1971). This apparent nest success rate is much higher than the actual success rate because successful nests are more likely to be located by researchers. Since most nests are not located until after incubation begins, even with radio-marked hens, one cannot account for the significant but unknown number of nests that are destroyed during the egg-laying period. That is why the Mayfield method (Mayfield 1961) was used to calculate actual nest survival rates for this study (Table 11). Although the survival rate of second nests (80.3%) falls within the range of nest success rates previously reported, the actual nest success rate in the entire population (first and second nests combined) is still below that range.

Reported egg hatchability rates in successful nests range from 90% to 97% (Bump et al. 1947:365, Cringan 1970, Fallis and Hope 1950, Fisher 1939, Rusch and Keith 1971). In the 1 study that attempted to distinguish between first and second nests egg hatchability was approximately 2% lower in second nests (Bump et al. 1947:365). This is comparable to the results from this study (Table 10), although egg hatchability in second nests was 12.6% below the hatchability in first nests. Bump et al. (1947:366-367) found that egg infertility rates nearly doubled and embryo mortality rates almost tripled in second nests. Egg infertility would be expected to increase if hens did not copulate again between laying their first and second clutches. The reasons for higher embryo mortality in second nests, however, remain unclear.

Chick Survival

Previous to this study, miniature radio transmitters had not been attached to ruffed grouse chicks. However, implanted transmitters similar to those used in this study were found to not significantly affect the growth or behavior of ring-necked pheasant chicks (Ewing et al. 1994). Also, Bakken et al. (1996) found that although mallard ducklings with externally attached miniature transmitters showed areas of increased surface temperature, neither implanted nor external transmitters had a biologically significant effect on thermoregulation.

Both attachment procedures used in the current study were deemed successful in terms of transmitter retention and minimal impact on chick survival. Although neither transmitter attachment procedure was believed to significantly reduce chick survival, there was a preference for the external suturing technique for several reasons. It required less time, equipment, and expertise than the implantation procedure. External attachment also did not require the wetting of chicks, and it involved less chance of accidental trauma to chicks during the procedure.

Chick survival estimates for the predispersal period in this study (~32%) are much lower than those reported by others. The summer survival rate of chicks was estimated to be 80% based on mean monthly brood sizes (Dorney and Kabat 1960). Comparing decreasing mean monthly brood sizes to the mean initial brood size at hatching yielded a survival estimate of 51% for the first 12 weeks of life (Rusch and Keith 1971). Bump et al. (1947:315) reported chick survival rates of just under 40% for the period from hatching to 31 August, but a description of their methods was lacking.

Chick mortality is highest during the first half of the predispersal period (Figure 11) (Bump et al. 1947:316). Therefore, if chick survival is estimated from mean brood sizes, the initial brood size estimated directly from an analysis of nesting success also should be used. If not, the survival estimate is inflated because much chick mortality occurs before many of the first brood observations are obtained. Due to this and the other disadvantages of using brood flush counts--variable sighting conditions, chronic underestimation of brood size, brood intermixing, and total brood loss--direct measures of chick survival should be favored.

Chick survival estimates in this study also do not include mortality that occurred during the first week after hatching. Brood size counts at the time of chick capture and transmitter attachment were attempted to account for mortality that occurred during the first week. These brood size estimates should be considered highly unreliable because of the large number of chicks and the extremely short amount of time they are able to be observed before hiding when flushed. Another possible solution is to attach transmitters to grouse chicks closer to the time of hatching. Smaller transmitters than the ones used in this study are available, but the battery life is significantly reduced. However, accurate estimation of chick survival is most important early in the predispersal period when there are the most chicks and chick mortality is highest.

It is difficult to determine the causes of chick mortality. Visible signs of a predator at the kill site are not as apparent during the summer as they are at other times of the year, such as when there are tracks or impressions in the snow in winter. Also, the abundance of feathers and other remains from the mortality of mature grouse that aid in the determination of the cause are usually not present after a chick mortality. Finally, the few remains that may be left by a predator (or the entire carcass of a chick dying from exposure) are quickly consumed by insects and other small scavengers that are most active during summer. Despite these problems it appears that avian predators are the most significant source of predispersal mortality (Table 12). Mammalian predators caused the second highest number of mortalities. Exposure and disease probably cause few chick mortalities.

Population Modeling

The discrepancy between summer production of grouse chicks/juveniles and fall-to-spring survival of females is small but remains significant because the grouse population was believed to be increasing, not just remaining steady, during the years when both estimates were made. Further analysis of the fall-to-spring data are necessary and will help in developing a more comprehensive and consistent year-round model. Future study of the proportion of hens that attempt second nests and a more refined estimate of chick survival, including an evaluation of transmitter retention rates, also will improve the model.

MANAGEMENT IMPLICATIONS

Ruffed grouse populations are typically managed through habitat management and hunting regulations. Fall grouse mortality due to hunting has been shown to be largely compensatory to other sources and has little direct effect on grouse recruitment (Fischer and Keith 1974; Gormley 1996; S. R. Winterstein, Mich. State Univ., unpubl. data). Grouse habitat, however, could be modified to improve recruitment.

If increasing grouse recruitment were a management objective, no forest harvest should occur during the nesting period because many grouse nests are located in mature, potentially harvestable stands. In addition, grouse nest near forest openings, which often consist of logging trails, and the increased human disturbance along the trails that accompanies forest harvest may reduce nest success and egg hatchability. Maximum nesting productivity would require that mature aspen trees, the preferred food source for incubating hens, be located within approximately 200 m of potential nesting areas. Brood habitat also could be improved to increase chick survival, but examination of brood habitat use and preference was beyond the scope of this study.

Predator exclusion should not be a goal of management from an ecosystem perspective. However, the control of mammalian predator populations within the limits of current hunting and trapping regulations almost certainly would increase the rates of nest success and chick survival.

The most significant implications for ruffed grouse management from this study are related to population modeling rather than field-oriented management applications. There is a search for the factors that limit the rebound of grouse populations from the low points in their 10-year cycle. So far, nearly all emphasis has been placed on fall-to-spring survival rates. This study has shown that nesting success and chick survival rates are substantially lower than previously estimated, suggesting that they may be limiting and deserve more consideration than they have been given thus far. Our understanding of annual ruffed grouse population dynamics will not be complete until the discrepancies between estimates of juvenile recruitment and age-and sex-specific fall-to-spring survival rates are resolved.

APPENDICES

APPENDIX A

APPENDIX A

FALL-TO-SPRING SURVIVAL

Fall-to-spring survival rates were determined for ruffed grouse at the HNF and PRCSF study sites from 1993 to 1998. As mentioned in the Methods section above, a complete discussion of fall trapping techniques were given by Clark (1996) and Gormley (1996). They also described the methods for year-round radio telemetry and fall-to-spring survival determination. A brief summary of the unpublished preliminary data that are relevant to the incorporation of nesting production and chick survival into a year-round population model is given here in Appendix A.

Comparisons of fall-to-spring survival rates were made between areas open and closed to hunting and between study sites. This was done to test the appropriateness of combining those samples of grouse to increase the sample size used in determining sex- and age-specific survival rates. Fall-to-spring survival rates were similar in areas open and closed to hunting at both study sites in the 3 years subsequent to 1993-94 (Table A1). Survival curves for those 3 years appeared to be more similar between study sites within the same year (Figures A1-A3) than among years within the same study site (Figures A4-A5). Formal testing revealed that the survival curves within each year were sufficiently similar between study sites for the samples to be combined (Table A2). Sex- and age-specific survival rates were calculated for each of the 3 years in which all the grouse in the study presumably came from the same underlying population (Table A3). The beginning and ending dates of the fall-to-spring period used in this analysis coincide with the end of the predispersal period (7 September) and the median date of first nest initiation (1 May), respectively.

APPENDIX A

Table A1. Log rank comparison of Kaplan-Meier survival functions for the period of 5 August to 15 May between areas open and closed to grouse hunting in northern Michigan in 1993-1997.

Site	Year	Open area survival rate	Closed area survival rate	X^2	*P*-value
HNF	1993-94	0.00	0.23	3.792	~0.05
	1994-95	0.40	0.37	1.310	>0.20
	1995-96	0.21	0.10	1.507	>0.20
	1996-97	0.37	0.35	0.527	~0.50
PRCSF	1993-94	0.19	0.63	6.380	<0.02
	1994-95	0.33	0.37	0.089	>0.70
	1995-96	0.25	0.11	1.052	~0.30
	1996-97	0.26	0.25	0.125	>0.70

APPENDIX A

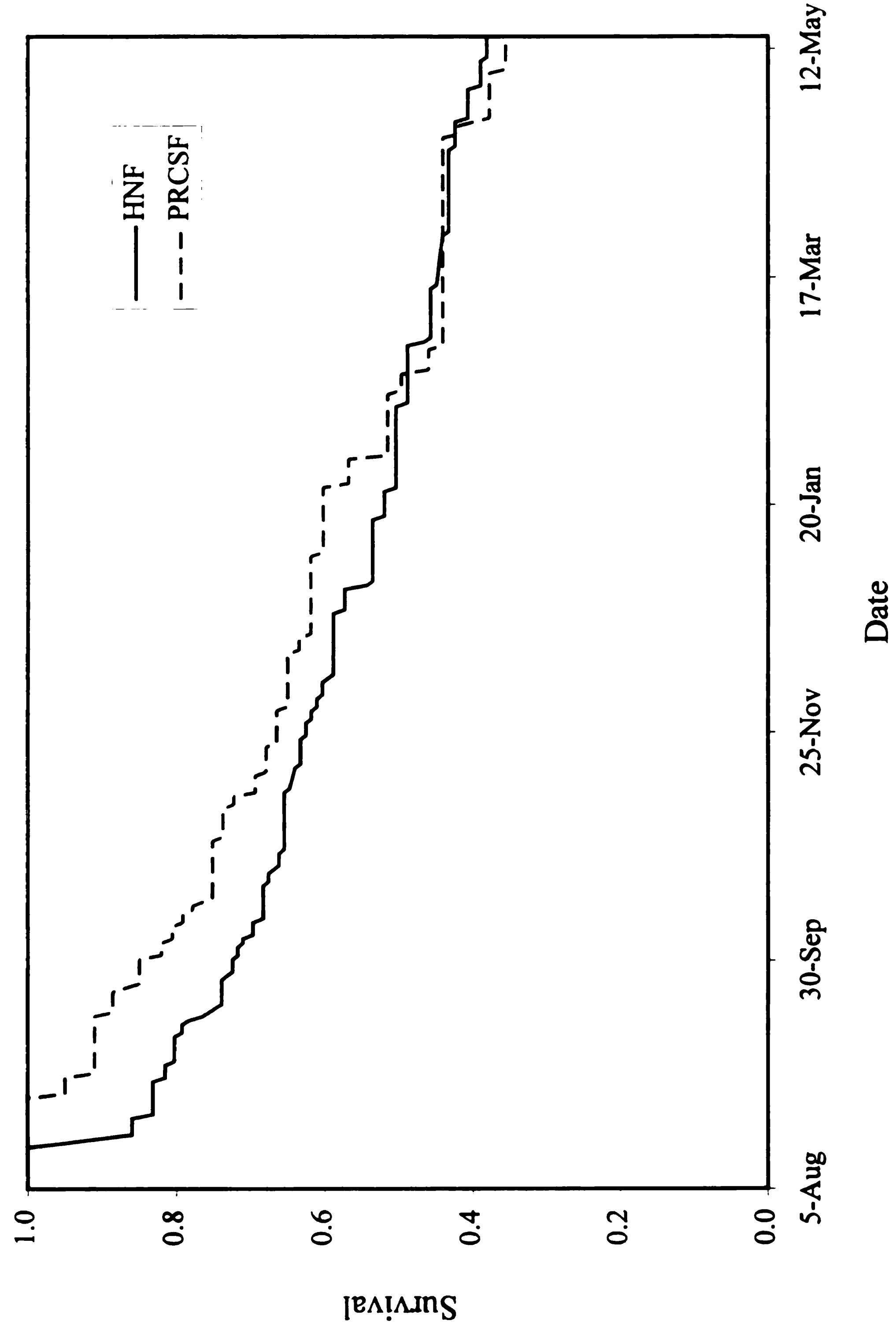

Figure A1. Kaplan-Meier survival rates of ruffed grouse in 2 study sites in northern Michigan for the fall-to-spring period in 1994-95.

APPENDIX A

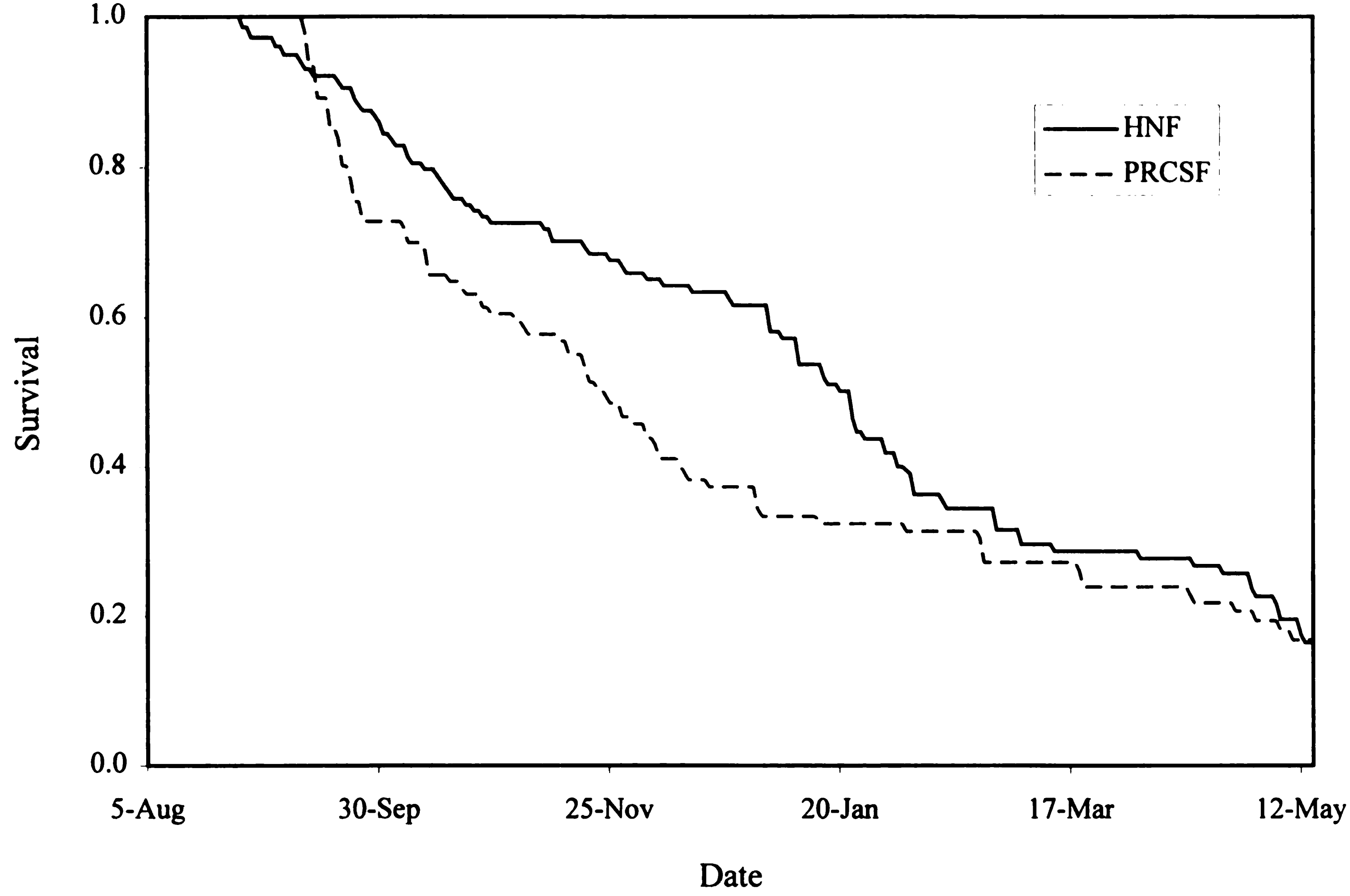

Figure A2. Kaplan-Meier survival rates of ruffed grouse in 2 study sites in northern Michigan for the fall-to-spring period in 1995-96.

APPENDIX A

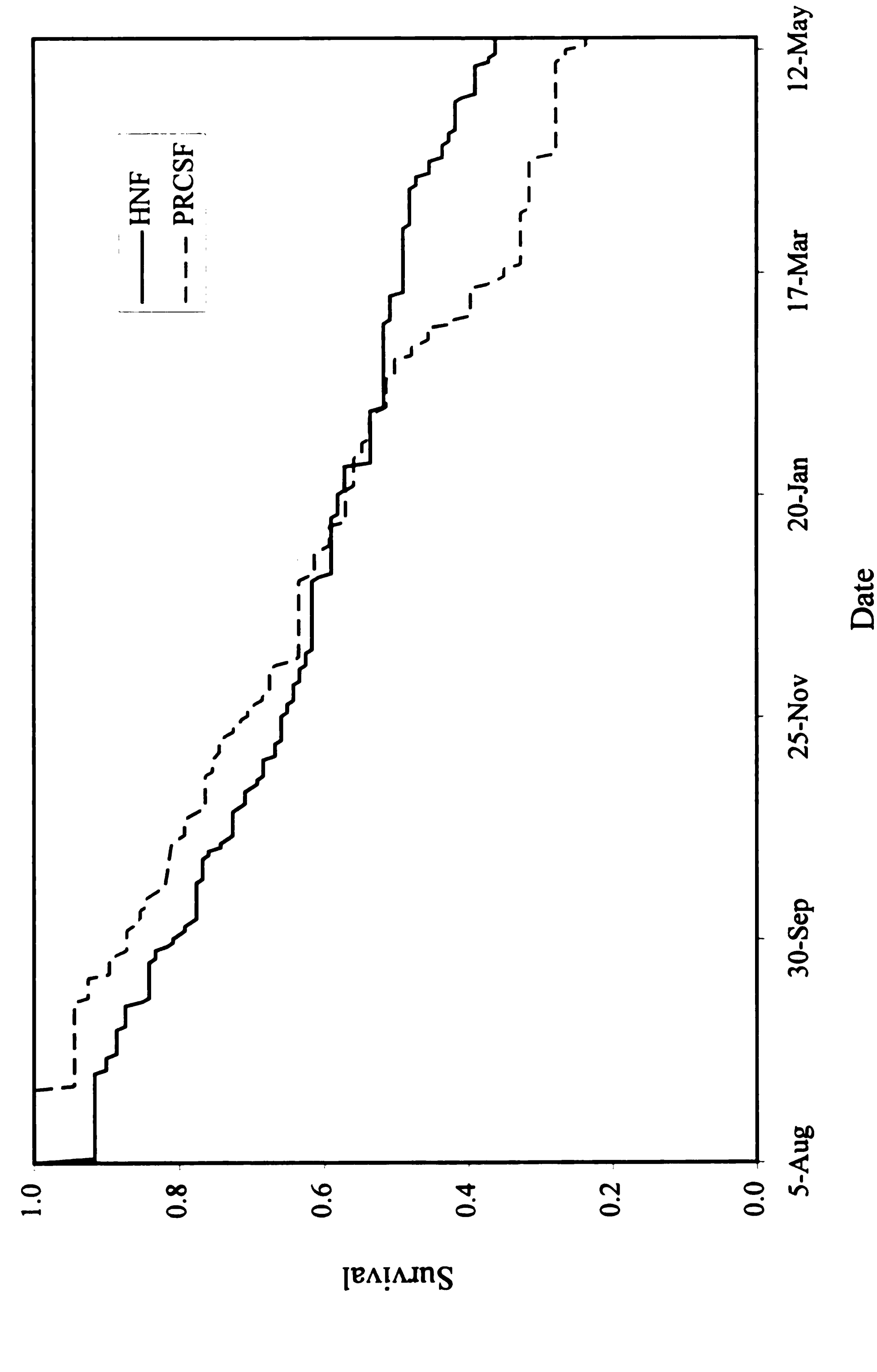

Figure A3. Kaplan-Meier survival rates of ruffed grouse in 2 study sites in northern Michigan for the fall-to-spring period in 1996-97.

APPENDIX A

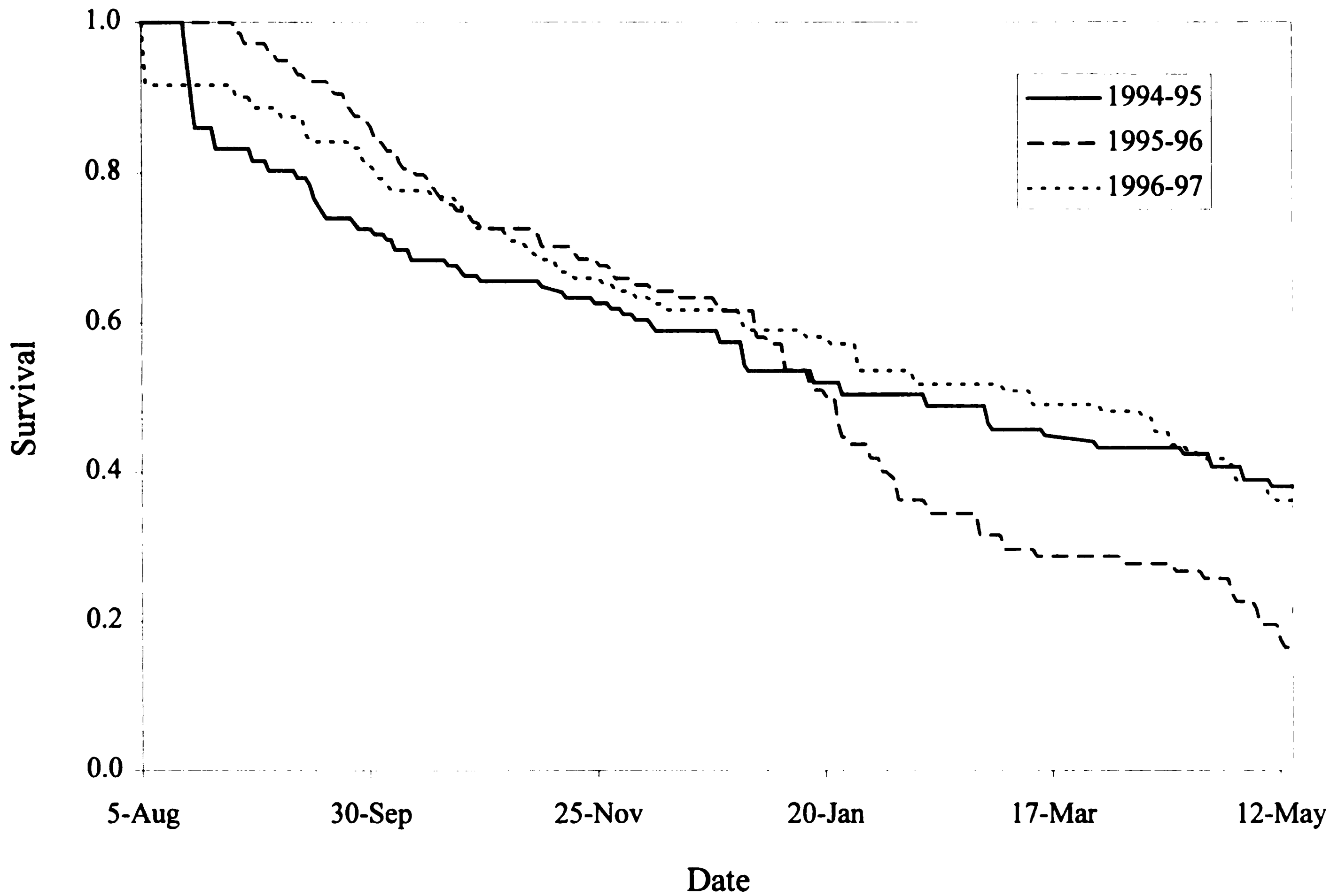

Figure A4. Kaplan-Meier survival rates of ruffed grouse in the Huron National Forest study site for the fall-to-spring periods from 1994 to 1997.

APPENDIX A

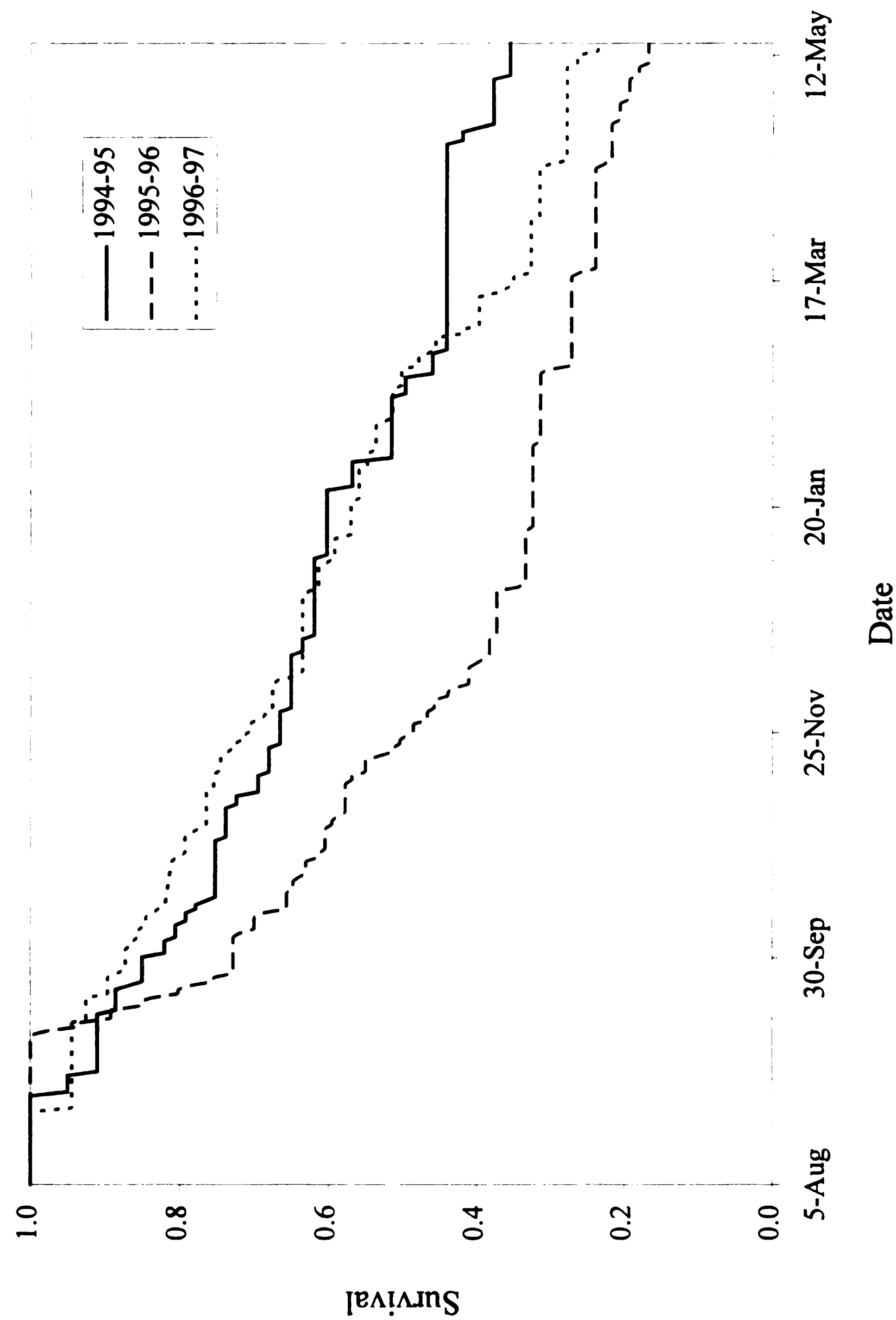

Figure A5. Kaplan-Meier survival rates of ruffed grouse in the Pigeon River Country State Forest study site for the fall-to-spring periods from 1994 to 1997.

APPENDIX A

Table A2. Log rank comparison of Kaplan-Meier survival functions for the period of 5 August to 15 May between study sites in northern Michigan in 1994-1997.

Year	HNF survival rate	PRCSF survival rate	X^2	*P*-value
1994-95	0.38	0.36	0.788	>0.30
1995-96	0.16	0.17	2.043	>0.10
1996-97	0.36	0.24	3.682	>0.05

APPENDIX A

Table A3. Kaplan-Meier survival rates for the period of 7 September to 1 May by sex and age of ruffed grouse in northern Michigan in 1994-1997.

	1994-95		1995-96		1996-97	
	n	Survival	n	Survival	n	Survival
Females						
Adults	35	0.61	29	0.32	29	0.38
Juveniles	58	0.53	78	0.17	64	0.47
All[a]	97	0.56	113	0.25	97	0.45
Males						
Adults	47	0.44	48	0.14	40	0.33
Juveniles	53	0.39	66	0.20	76	0.29
All[a]	103	0.41	122	0.16	119	0.30

[a] Includes grouse of known sex but unknown age.

APPENDIX B

APPENDIX B

ORIGINAL DATA

Table B1. Original categorical data for ruffed grouse nest sites in northern Michigan in 1996 and 1997.

Date sampled	Hen number	Nesting attempt	Hen age[a]	Site[b]	Vegetation type[c]	Nest object	Nest object type[d]	Orientation from nest object[e]	Slope aspect[f]
6/11/96	66	1	Y	HO	j.p.	trees	beech	NE	
6/11/96	72	1	uk	HO	oak	logs	uk	S	SW
6/15/96	140	1	A	HO	r.p.	tree	ironw.	S	SE
6/11/96	143	1	A	HO	aspen	tree	maple	S	
6/11/96	146	1	A	HO	aspen	tree	j.p.	N	
6/12/96	173	1	A	HO		tree	birch	E	
6/11/96	196	1	Y	HO	j.p.	snag	j.p.	E	
8/7/96	4752	1	A	PC	w.p.	trees	maple	S	
8/7/96	6124	2	A	PC	r.p.	tree	w.p.	W	
8/7/96	4641	1	A	PO	aspen	tree	b. fir	SW	SW
8/7/96	4641	2	A	PO	aspen	tree	b. fir	N	
8/7/96	6024	1	A	PO	low	tree	b. fir	E	E
6/20/97	2022	1	Y	HC	aspen	tree	aspen	SE	NE
6/13/97	2036	1	Y	HC	aspen	branch	uk	E	SW
6/13/97	2106	1	Y	HC	j.p.	log	j.p.		SE
7/3/97	2106	2	Y	HC	oak/h.	snag	aspen	NW	SE
6/20/97	2120	1	Y	HC	oak/h.	log	uk	S	S
6/13/97	2204	1	Y	HC	aspen	branch	uk	SW	
6/13/97	2209	1	Y	HC	aspen	tree	maple	NE	E
6/20/97	2680	1	Y	HC	j.p./oak	tree	oak	S	
6/20/97	2685	1	Y	HC	oak/h.	tree	maple	N	NE

APPENDIX B

Table B1 (cont'd)

Date sampled	Hen number	Nesting attempt	Hen age[a]	Site[b]	Vegetation type[c]	Nest object	Nest object type[d]	Orientation from nest object[e]	Slope aspect[f]
6/16/97	0	1	uk	HO	aspen	tree	aspen	N	
6/11/97	57	1	A	HO	aspen	log	aspen		W
6/16/97	140	1	A	HO	j.p.	tree	oak	E	
7/1/97	173	1	A	HO		trees	aspen	W	
6/16/97	242	1	Y	HO	oak	tree	aspen	E	
6/11/97	245	1	Y	HO	j.p.	snag	aspen	SW	
6/16/97	268	1	Y	HO	aspen	tree	aspen	W	
6/16/97	303	1	A	HO	aspen	snag	aspen	E	SE
6/16/97	316	1	Y	HO	r.p.	branch	oak		N
6/16/97	326	1	Y	HO	aspen	tree	aspen	W	
6/11/97	329	1	Y	HO	j.p.	tree	j.p.	S	N
6/11/97	339	1	Y	HO	oak/h.	tree	r.p.	S	
7/7/97	6063	2	Y	PC	grass	tree	w.p.	W	
7/7/97	6078	1	A	PC		log	uk		
7/7/97	6078	2	A	PC		stump	uk	NE	
7/7/97	6371	1	A	PC	r.p.	tree	aspen	SW	
7/7/97	6371	2	A	PC	s. conif.	stump	uk	N	
7/7/97	4654	1	A	PO	maple	tree	maple	NW	SE
7/7/97	6024	1	A	PO	low	snag	cedar	SE	SE

[a] Y = yearling, A = adult, uk = unknown.
[b] HO = HNF open area, HC = HNF closed area, PO = PRCSF open area, PC = PRCSF closed area.
[c] j.p. = jack pine, r.p. = red pine, w.p. = white pine, low = lowland brush, h. = hickory, s. conif. = swamp conifer, blank indicates nest was on private property.
[d] ironw. = ironwood, b. fir = balsam fir, j.p. = jack pine, r.p. = red pine, w.p. = white pine, uk = unknown.
[e] N = north, NE = northeast, E = east, SE = southeast, S = south, SW = southwest, W = west, NW = northwest, blank indicates nest was directly beneath the log or branch.
[f] Blank indicates nest was on level ground. Abbreviations are the same as for the previous variable.

APPENDIX B

Table B2. Original interval data for ruffed grouse nest sites in northern Michigan in 1996 and 1997.

Date sampled	Hen number	Nesting attempt	Stand age (yr)[a]	Nest object size, dbh[b] (cm)	Stem density (# / ha)	Horizontal cover from 5 m (%)	Horizontal cover from 15 m (%)	Ground cover (%)	Canopy cover (%)	Distance to nearest opening (m)	Distance to nearest aspen (m)	Distance to nearest conifer (m)
6/11/96	66	1	69	10	4100	5	40	30	95	46	2	66
6/11/96	72	1	76	7	21000	80	100	80	94	21	43	30
6/15/96	140	1	51	5	7700	40	55	70	86	224	2	2
6/11/96	143	1	23	8	13600	25	80	55	98	7	2	285
6/11/96	146	1	23	10	10800	25	90	55	86	2	6	0
6/12/96	173	1		11	5300	30	100	45	87	20	6	1
6/11/96	196	1	75	30	3000	10	70	50	73	235	31	3
8/7/96	4752	1	81	3	7800	85	100	60	98	4	160	1
8/7/96	6124	2		18	4200	80	95	65	93	2	83	0
8/7/96	4641	1	57		3800	50	85	60	86	6	5	0
8/7/96	4641	2	24		2700	100	100	65	85	24	35	0
8/7/96	6024	1			30200	70	100	85	73	70	72	0
6/20/97	2022	1	15	6	7600	50	100	75	93	30	38	125
6/13/97	2036	1	3	10	6200	35	90	55	82	19	6	45
6/13/97	2106	1	3	10	2200	50	65	35	51	1	192	5
7/3/97	2106	2	18	10	8000	75	90	35	88	7	160	6
6/20/97	2120	1	13	5	12000	25	100	50	86	6	100	150
6/13/97	2204	1	14	2	9200	60	100	65	59	2	16	18
6/13/97	2209	1	39	4	5600	35	75	65	91	17	4	17
6/20/97	2680	1	16	8	20500	25	100	40	95	50	75	0
6/20/97	2685	1	13	1	6700	45	70	50	82	9	42	4

APPENDIX B

Table B2 (cont'd)

Date sampled	Hen number	Nesting attempt	Stand age (yr)[a]	Nest object size, dbh[b] (cm)	Stem density (# / ha)	Horizontal cover from 5 m (%)	Horizontal cover from 15 m (%)	Ground cover (%)	Canopy cover (%)	Distance to nearest opening (m)	Distance to nearest aspen (m)	Distance to nearest conifer (m)
6/16/97	0	1	23	10	13500	45	80	45	99	22	3	4
6/11/97	57	1	68	15	8400	35	75	55	94	33	3	96
6/16/97	140	1	40	2	10300	25	100	35	83	15	165	1
7/1/97	173	1		12	4300	80	95	85	98	4	6	5
6/16/97	242	1	73	17	9100	50	85	15	96	27	0	152
6/11/97	245	1	24	4	9400	35	55	40	90	13	1	2
6/16/97	268	1	24	17	3900	35	55	35	96	58	0	31
6/16/97	303	1	74	13	2700	25	35	40	97	20	6	0
6/16/97	316	1	73	2	3100	45	90	50	88	5	107	1
6/16/97	326	1	22	14	6500	70	100	55	95	18	2	85
6/11/97	329	1		15	4200	25	40	30	90	4	14	0
6/11/97	339	1	70	20	3500	55	75	40	94	3	57	0
7/7/97	6063	2		35	1300	40	45	55	97	3	6	0
7/7/97	6078	1		10	3100	75	100	100	83	35	1	5
7/7/97	6078	2		30	3200	45	75	45	87	11	9	2
7/7/97	6371	1	71	22	2400	15	25	30	94	116	0	1
7/7/97	6371	2	82	25	2000	60	100	85	89	4	9	2
7/7/97	4654	1			4600	5	5	15	99	60	80	240
7/7/97	6024	1		13	24400	30	80	55	87	13	110	2

[a] A blank indicates that stand age was not available because it was privately owned, had never been harvested, or was of mixed age.
[b] Diameter at breast height of the object against which hens positioned their nest. Blank indicates missing data.

APPENDIX B

Table B3. Original data for nesting parameters of ruffed grouse in northern Michigan in 1996 and 1997.

Year	Study site[a]	Hen number	Hen age[b]	Nesting attempt	Nest fate[c]	Clutch size[d]	Eggs hatched	Day of nest initiation[e]	Day of incubation initiation[e]	Day nest ended[e]	Observed incubation time (days)[f]	Days under observation
1996	HO	66	Y	1	A		0	128		138		3
1996	HO	72	uk	1	D	12	0	122	136	156		22
1996	HO	140	A	1	S	13	12	125	140	165		18
1996	HO	143	A	1	S	13	13	123	138	162	24	27
1996	HO	146	A	1	S	13	13	120	135	160		21
1996	HO	173	A	1	S	14	13	120	137	162		18
1996	HO	196	Y	1	A	13	0	121	136	160		28
1996	PC	4752	A	1	S	11	11	134	147	172		9
1996	PC	6124	A	2	S	8	7	140	149	174		26
1996	PO	4641	A	1	D	10	0			149		13
1996	PO	4641	A	2	S	8	7	155	164	185	21	23
1996	PO	6024	A	1	S	12	12	122	136	161		18
1997	HO	57	A	1	S	13	13	116	131	156		15
1997	HO	140	A	1	S	13	11	123	138	163		22
1997	HO	173	A	1	S	12	12	134	148	173		28
1997	HO	242	Y	1	S	13	13	120	135	160	25	27
1997	HO	245	Y	1	D		0	127		146		13
1997	HO	268	Y	1	S	14	14	117	134	161	27	28
1997	HO	303	A	1	S	16	16	118	137	162		20
1997	HO	316	Y	1	S	13	13	117	132	157		19
1997	HO	326	Y	1	S	13	13	121	136	161		22
1997	HO	329	Y	1	S	12	12	116	130	155		6
1997	HO	339	Y	1	D	10	0			156		11

Table B3 (cont'd)

Year	Study site[a]	Hen number	Hen age[b]	Nesting attempt	Nest fate[c]	Clutch size[d]	Eggs hatched	Day of nest initiation[e]	Day of incubation initiation[e]	Day nest ended[e]	Observed incubation time (days)[f]	Days under observation
1997	HC	2022	Y	1	S	12	12	123	137	162		23
1997	HC	2036	Y	1	A	12	0			151		11
1997	HC	2106	Y	1	D		0			142		2
1997	HC	2106	Y	2	S	7	5	148	156	182	26	28
1997	HC	2120	Y	1	S	11	11	123	136	161		21
1997	HC	2204	Y	1	S	13	5	119	134	159		27
1997	HC	2209	Y	1	S	14	14	116	133	158		18
1997	HC	2680	Y	1	S	11	11	123	136	161		22
1997	HC	2685	Y	1	S	12	12	117	131	156		23
1997	PC	6352	Y	1	D	17	0			146		7
1997	PC	6063	Y	2	S	6	4	145	152	177		25
1997	PC	6078	A	1	D		0			145		6
1997	PC	6078	A	2	D	8	0	151	160	176		23
1997	PC	6371	A	1	D	12	0			148		10
1997	PC	6371	A	2	S	7	7	151	159	184		24
1997	PO	4654	A	1	S	16	16	117	136	161		26
1997	PO	6024	A	1	S	12	12	116	130	155		20

[a] HO = HNF open area, HC = HNF closed area, PO = PRCSF open area, PC = PRCSF closed area.
[b] Y = yearling, A = adult, uk = unknown.
[c] S = successful, D = destroyed, A = abandoned (hen was killed, nest not destroyed).
[d] A blank indicates that the clutch was not known to be complete at the time of nest destruction or abandonment.
[e] Day of the year from 1 January. 1 May = 121, 1 June = 152, and 1 July = 182. A blank indicates that the day was not able to be determined.
[f] A blank indicates that the duration was not able to be determined.

APPENDIX B

Table B4. Original data for ruffed grouse chicks captured in northern Michigan in 1996.

Chick number	Age at capture (days)[a]	Weight at capture (g)	Hen number	Study site[b]	Radio type[c]	Capture date	Date out of study	Status[d]	Source of mortality[e]
1	5-6	20.0	6024	PO	S	6/14/96	6/21/96	mortality	no diag.
2	6	23.0	146	HO	I	6/14/96	6/16/96	radio only	no diag.
3	6	24.5	146	HO	S	6/14/96	6/16/96	mortality	mammal
4	5	17.0	143	HO	I	6/15/96	6/29/96	radio only	no diag.
5	5	18.0	143	HO	I	6/15/96	7/16/96	censored	
6	5	16.5	143	HO	S	6/15/96	6/28/96	radio only	no diag.
7	10	30.0	143	HO	S	6/20/96	7/18/96	mortality	mammal
8	7	20.5	140	HO	I	6/20/96	6/23/96	mortality	avian
9	7	21.0	140	HO	S	6/20/96	9/18/96	mortality	avian
10	10	42.5	173	HO	I	6/20/96	9/1/96	mortality	avian
11	10	43.0	173	HO	S	6/20/96	6/21/96	mortality	stress
12	uk	20.0	1	HO	I	6/21/96	7/13/96	radio only	no diag.
13	uk	21.5	1	HO	I	6/21/96	7/9/96	radio only	no diag.
14	uk	22.0	1	HO	S	6/21/96	9/18/96	censored	
15	11	34.0	143	HO	S	6/21/96	9/14/96	censored	
16	uk	29.0	1	HO	S	6/24/96	7/3/96	mortality	avian
17	6-7	24.0	4752	PC	I	6/25/96	10/9/96	censored	
18	6-7	21.0	4752	PC	I	6/25/96	7/8/96	mortality	mammal
19	6-7	28.0	4752	PC	S	6/25/96	7/15/96	mortality	avian
20	6-7	27.0	4752	PC	S	6/25/96	7/15/96	mortality	avian
21	5	17.0	6124	PC	I	6/27/96	8/25/96	radio only	no diag.
22	5	17.0	6124	PC	I	6/27/96	8/25/96	radio only	no diag.
23	5	16.5	6124	PC	S	6/27/96	10/2/96	censored	
24	5	16.0	6124	PC	S	6/27/96	10/9/96	censored	
25	7	21.5	6124	PC	I	6/29/96	8/12/96	censored	
26	7	22.5	6124	PC	I	6/29/96	7/31/96	radio only	no diag.

[a] uk = unknown age because the chicks were from a nest that was not under observation.
[b] HO = HNF open area, PO = PRCSF open area, PC = PRCSF closed area.
[c] S = sutured externally, I = implanted.
[d] radio only = only an unmarked transmitter was collected; presumed mortality.
[e] no diag. = no diagnosis, stress = exposure or stress due to capture.

APPENDIX B

Table B5. Original data for ruffed grouse chicks captured in northern Michigan in 1997.

Chick number	Age at capture (days)	Weight at capture (g)	Hen number	Study site[a]	Radio type[b]	Capture date	Date out of study	Status[c]	Source of mortality[d]
27	5	18.5	329	HO	S	6/9/97	10/7/97	censored	
28	5	18.5	329	HO	S	6/9/97	6/14/97	mortality	no diag.
29	5	19.0	329	HO	S	6/9/97	6/26/97	mortality	avian
30	5	19.0	329	HO	S	6/9/97	9/10/97	censored	
31	5-6	20.0	57	HO	S	6/10/97	8/26/97	censored	
32	5-6	19.5	57	HO	S	6/10/97	7/25/97	mortality	avian
33	7-8	23.0	57	HO	S	6/12/97	8/23/97	censored	
34	6	20.5	2209	HC	S	6/13/97	6/21/97	mortality	avian
35	6	19.5	2209	HC	S	6/13/97	6/23/97	radio only	no diag.
36	6	22.5	2209	HC	S	6/13/97	6/21/97	radio only	no diag.
37	6	19.5	2209	HC	S	6/13/97	9/6/97	censored	
38	6	20.5	2209	HC	S	6/13/97	6/27/97	mortality	avian
39	6	20.5	2209	HC	S	6/13/97	6/27/97	mortality	avian
40	8-9	22.5	316	HO	S	6/15/97	9/21/97	censored	
41	8-9	21.5	316	HO	S	6/15/97	8/12/97	mortality	no diag.
42	8-9	20.5	316	HO	S	6/15/97	7/22/97	mortality	avian
43	6	26.0	242	HO	S	6/15/97	7/6/97	radio only	no diag.
44	6	24.5	242	HO	S	6/15/97	8/16/97	censored	
45	6	23.5	242	HO	S	6/15/97		alive[e]	
46	6	26.5	242	HO	S	6/15/97	7/3/97	mortality	avian
47	6	21.0	268	HO	S	6/16/97	7/4/97	mortality	mammal
48	6	21.5	268	HO	S	6/16/97	8/16/97	censored	
49	6	21.5	268	HO	S	6/16/97	6/26/97	mortality	stress
50	6	23.0	268	HO	S	6/16/97	7/11/97	mortality	avian
51	6	21.0	268	HO	S	6/16/97	6/26/97	mortality	mammal
52	6	23.5	303	HO	S	6/17/97	9/3/97	censored	
53	6	23.0	303	HO	S	6/17/97	6/23/97	mortality	avian
54	6	25.0	303	HO	S	6/17/97	7/6/97	mortality	avian
55	6	24.0	303	HO	S	6/17/97	6/29/97	mortality	avian
56	6-7	29.5	2680	HC	S	6/17/97	9/26/97	censored	
57	7	23.5	2120	HC	S	6/17/97	9/16/97	censored	
58	7	24.5	2120	HC	S	6/17/97	6/21/97	mortality	avian
59	7	25.0	2120	HC	S	6/17/97	7/16/97	mortality	mammal

APPENDIX B

Table B5 (cont'd)

Chick number	Age at capture (days)	Weight at capture (g)	Hen number	Study site[a]	Radio type[b]	Capture date	Date out of study	Status[c]	Source of mortality[d]
60	6	28.5	2022	HC	S	6/17/97	9/6/97	censored	
61	6	24.5	2022	HC	S	6/17/97	6/24/97	radio only	no diag.
62	6	26.0	2022	HC	S	6/17/97	7/4/97	radio only	no diag.
63	6	25.5	2022	HC	S	6/17/97	7/1/97	mortality	avian
64	6	19.0	140	HO	S	6/18/97	7/23/97	radio only	no diag.
65	6	18.5	140	HO	S	6/18/97	7/2/97	mortality	avian
66	6	20.0	140	HO	S	6/18/97	6/23/97	radio only	no diag.
67	6	17.0	140	HO	S	6/18/97	9/14/97	censored	
68	6	19.5	140	HO	S	6/18/97	7/12/97	mortality	avian
69	6	20.0	140	HO	S	6/18/97	9/14/97	censored	
70	8	26.5	2120	HC	S	6/18/97	6/21/97	mortality	avian
71	7	29.5	2022	HC	S	6/18/97	7/19/97	mortality	avian
72	7	28.0	303	HO	S	6/18/97	9/3/97	censored	
73	7	29.5	303	HO	S	6/18/97	7/23/97	censored	
74	6	27.0	173	HO	S	6/28/97	7/11/97	radio only	no diag.
75	6	25.0	173	HO	S	6/28/97	7/7/97	mortality	avian
76	6	26.0	173	HO	S	6/28/97	7/4/97	mortality	mammal

[a] HO = HNF open area, HC = HNF closed area.
[b] S = sutured externally.
[c] radio only = only an unmarked transmitter was collected; presumed mortality.
[d] no diag. = no diagnosis, stress = exposure or stress due to capture.
[e] Chick #45 was recaptured by nightlighting on 25 August 1997, was fitted with a bib-type transmitter, and was known to be alive as of 1 March 1998.

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LITERATURE CITED

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