Ruffed grouse productivity and habitat selection at the base of the Beartooth Plateau in southcentral Montana

by David Edward Johnson

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fish and Wildlife Management
Montana State University

Abstract:
Little is known about the ecology of ruffed grouse (Bonasa umbellus) in the Northern Rockies. In particular, very little is known about the nesting and brood-rearing ecology of this species in habitats consisting of aspen (Populus tremuloides)/conifer mosaics, such as those found in southcentral Montana. Therefore, I studied nesting and brood-rearing hens at the base of the Beartooth Plateau in Luther and Dean, Montana with the objectives of estimating nesting and brood-rearing parameters, habitat selection during these periods, and how habitat selection influences productivity. Using radio-marked hens, I located and monitored 12 nests and 5 broods during the spring and summer of 1997 and 1998. Nesting success over the two year period was 0.42 (SE = 0.15). Although aspen cover type was selected for nesting more than expected at random ($P = 0.08$), nesting success did not differ between cover types ($P = 0.92$). No differences in characteristics at successful and unsuccessful nests were detected ($P = 0.10$). However, nest sites contained more Cottonwood (Populus spp.) stems ($P < 0.01$) than did random sites. Mean chick survival was 0.37 (SE = 0.03). Brood sites had denser shrub and ground cover, higher canopy closure, fewer lodgepole pine stems, more aspen stems, and were closer to water than were random sites ($P < 0.01$). While aspen cover type was preferred by broodrearing hens ($P = 0.08$) and was positively correlated with chick survival, coniferous cover types were avoided ($P = 0.08$) and negatively correlated with chick survival. Broods that used upland stands with dense shrub understory had greater chick survival ($P = 0.10$). Results of this study suggest that productivity may be improved by regenerating aspen stands and their associated understories. Although aspen was neutral habitat in terms of nesting success, the pattern of nest-site selection suggests a historical advantage to hens nesting in aspen. However, recent forest-management activities may have increased predator contact with hens nesting in aspen by reducing the amount of aspen on the landscape. Higher chick-survival rates for broods using areas with denser understories is likely due to a decrease in predator contact. Differences in survival and habitat use exist between this study and studies from the midwestern and eastern United States. However, the similarities discovered suggest that management practices used in these areas may be applicable to the Northern Rockies. However, because of small sample sizes in this study, future research on ruffed grouse ecology should be conducted in the Northern Rockies to develop appropriate management strategies.

RUFFED GROUSE PRODUCTIVITY AND HABITAT SELECTION AT THE BASE OF THE BEARTOOTH PLATEAU IN SOUTHCENTRAL MONTANA

by

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David Edward Johnson

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

Little is known about the ecology of ruffed grouse (Bonasa umbellus) in the Northern Rockies. In particular, very little is known about the nesting and brood-rearing ecology of this species in habitats consisting of aspen (Populus tremuloides)/conifer mosaics, such as those found in southcentral Montana. Therefore, I studied nesting and brood-rearing hens at the base of the Beartooth Plateau in Luther and Dean, Montana with the objectives of estimating nesting and brood-rearing parameters, habitat selection during these periods, and how habitat selection influences productivity. Using radio-marked hens, I located and monitored 12 nests and 5 broods during the spring and summer of 1997 and 1998. Nesting success over the two year period was 0.42 (SE = 0.15). Although aspen cover type was selected for nesting more than expected at random (P = 0.08), nesting success did not differ between cover types (P = 0.92). No differences in characteristics at successful and unsuccessful nests were detected (P= 0.10). However, nest sites contained more Cottonwood (Populus spp.) stems (P < 0.01) than did random sites. Mean chick survival was 0.37 (SE = 0.03). Brood sites had denser shrub and ground cover, higher canopy closure, fewer lodgepole pine stems, more aspen stems, and were closer to water than were random sites (P < 0.01). While aspen cover type was preferred by brood-rearing hens (P = 0.08) and was positively correlated with chick survival, coniferous cover types were avoided (P = 0.08) and negatively correlated with chick survival. Broods that used upland stands with dense shrub understory had greater chick survival (P = 0.10). Results of this study suggest that productivity may be improved by regenerating aspen stands and their associated understories. Although aspen was neutral habitat in terms of nesting success, the pattern of nest-site selection suggests a historical advantage to hens nesting in aspen. However, recent forest-management activities may have increased predator contact with hens nesting in aspen by reducing the amount of aspen on the landscape. Higher chick-survival rates for broods using areas with denser understories is likely due to a decrease in predator contact. Differences in survival and habitat use exist between this study and studies from the midwestern and eastern United States. However, the similarities discovered suggest that management practices used in these areas may be applicable to the Northern Rockies. However, because of small sample sizes in this study, future research on ruffed grouse ecology should be conducted in the Northern Rockies to develop appropriate management strategies.

INTRODUCTION

The ruffed grouse is one of the most wide ranging and racially variable of all North American Tetraonids. Its 13 subspecies range from Alaska across Canada and the northern United States to Maine and south to Georgia (Aldrich 1963). Throughout their geographic range, ruffed grouse are generally associated with deciduous habitats (Aldrich 1963), especially those containing an aspen component (Svoboda and Gullion 1972). The relationship between aspen and ruffed grouse has been well documented in many parts of their range. Svoboda and Gullion (1972) reported preferential use of aspen by breeding ruffed grouse in southeastern Minnesota. Bump et al. (1947) discovered second growth hardwoods were preferred by nesting hens in upstate New York, while Maxson (1974) reported that mixed hardwood stands containing aspen were preferred for nesting in southeastern Minnesota. In central Wisconsin, Kubisiak (1978) found that brood-rearing hens clearly preferred aspen sapling stands, and both Landry (1982) and Rusch and Keith (1971b) reported the presence of aspen in the over-story canopy at ≥ 90% of brood flush sites in central Utah and central Alberta. Aspen has also been reported as preferred by foraging grouse during winter months in eastcentral Minnesota (Huempfner and Tester 1988) and northern Utah (Phillips 1967).

Although numerous studies have addressed the relationship between aspen and ruffed grouse, most studies investigating ruffed grouse ecology have been conducted in the Eastern and Midwestern United States. On most of these study areas, aspen was abundant or existed in large, contiguous forests. Few studies regarding ruffed grouse ecology have been conducted in areas with different ecosystem characteristics. In particular, very little is known about habitat preferences and the relationship between aspen and ruffed grouse productivity in the Northern Rockies where aspen stands are relatively smaller and more fragmented than their eastern and midwestern counterparts. Whereas aspen stands in the Northern Rockies rarely exceed 2ha in size (Mueggler 1985), aspen stands in other parts of the country can exceed 100ha (Yahner and Scott 1988). Because insufficient data concerning characteristics of habitat use by ruffed grouse exist for the Northern Rockies, it is difficult to draw parallels with other studies. Therefore, the applicability of published management strategies for ruffed grouse is unknown in the Northern Rockies until a better understanding of ruffed grouse ecology in this area is realized.

Population dynamics of grouse are most affected by breeding success, especially nesting success. Variation in breeding success has been positively correlated with population changes between years in several grouse populations (Beregerud 1988a). Bergerud (1988a) stated that nesting success of grouse is the most variable parameter in the dynamics of their populations and contributes more to changes in population size between years than does any other parameter. Results from other studies (Bump et al.1947, Maxson 1974, Kupa 1966) suggest that nesting success varies among geographic regions and among habitats used for nesting. To the best of my knowledge, there are currently no published estimates of nesting success for the Northern Rockies. Therefore, a better understanding of nest-site selection and its effect on nesting success in habitats within aspen-conifer mosaics such as those found in the Northern Rockies is essential to managers interested in increasing ruffed grouse productivity.

The second critical factor in breeding success is chick survival (the proportion of chicks that survive their first summer). Surviving chicks indicate levels of both breeding production and potential recruitment into the breeding population the following spring. Despite the importance of this parameter to grouse population dynamics, only a few studies have estimated chick survival (Bump et al. 1947, Rusch and Keith 1971a, Kupa 1966), with estimates ranging from 27% to 51%. Because chick survival appears to differ among localities and affect productivity, it is necessary to estimate chick survival to accurately assess local ruffed grouse productivity. As for nesting success, no chick survival estimates are available for the Northern Rockies.

Along with chick survival rates, managers interested in improving ruffed grouse productivity also need to better understand the effect that brood-rearing habitat has on chick survival. Although numerous studies have investigated habitat use by grouse ruffed broods (Rusch and Keith 1971b, Porath and Vohs 1972, Landry 1982, Stouffer and Peterson 1985), none has adequately addressed the relationship between habitat use and chick survival. Therefore, the effect of specific habitat characteristics used during the brood-rearing period on chick survival remains speculative. Due to this paucity of information regarding chick survival, emphasis should be placed on obtaining a better understanding of brood-site selection and its effect on chick survival in order to estimate what constitutes quality brood-rearing habitat. Because habitat characteristics vary considerably across the range of ruffed grouse, determining quality habitat should be undertaken at local scales.

Despite research efforts in other areas of the ruffed grouse's geographic range, managers in the Northern Rockies do not have sufficient information on nest success, chick survival and the hypothesized importance of aspen to these population parameters to adequately manage for this species. A better understanding of nest success and its relationship to nest site habitat characteristics and of chick survival and its relationship to brood site habitat characteristics is necessary for effective ruffed grouse management. I therefore designed this study with the following objectives: (1) estimate breeding success by estimating nest success and chick survival; (2) estimate habitat use and habitat selection by nesting hens; (3) use nest-site habitat selection and habitat-specific nest success to estimate habitat quality; (4) estimate habitat use and selection by brood-rearing hens; and (5) use brood-site habitat selection and habitat- specific chick survival to estimate habitat quality.

STUDY AREA

My study was conducted in south central Montana at the base of the Beartooth Plateau in the Custer National Forest (Figure 1). This area is representative of forested portions of southern Montana and provides the unique opportunity to examine the hypothesized importance of aspen in an area where aspen is found in small, patchy stands among conifers. Two separate study sites, Red Lodge Creek drainage (RLC) and Little Rocky Creek drainage (LRC) were established (Fig. 1). Delineation of study-site boundaries were based on identification of physical barriers to dispersal and expected average dispersal distances as reported in the literature (Hale and Dorney 1963, Godfrey and Marshall 1969).

RLC drainage was located 19 km west of Red Lodge in Carbon County, Montana. RLC was 24.88 km^2, ranged in elevation from 1,790 m to 2,200 m. RLC was dominated by lodgepole pine (Pinus contorta), with aspen stands $\leq$ 2 ha interspersed throughout. Douglas fir (Pseudotsuga menziesii), Subalpine fir (Abies lasiocarpa), Englemann spruce (Picea engelmannii), Ponderosa pine (Pinus ponderosa), and Whitebark pine (Pinus albicaulus) were found in limited proportions throughout the study site. Alder (Alnus incana) and Cottonwood (Populus spp.) were found in moderate abundances along creek bottoms. Meadows of bunchgrass/forbes were also interspersed throughout the study site. Dominant shrubs included snowberry (Symphoricarpus albus), ninebark (Physocarpus malvaceus), rose (Rosa woodsii), serviceberry (Amelanchier alnifolia), buffaloberry (Shepherdia canadensis), and spirea (Spirea betulifolia).

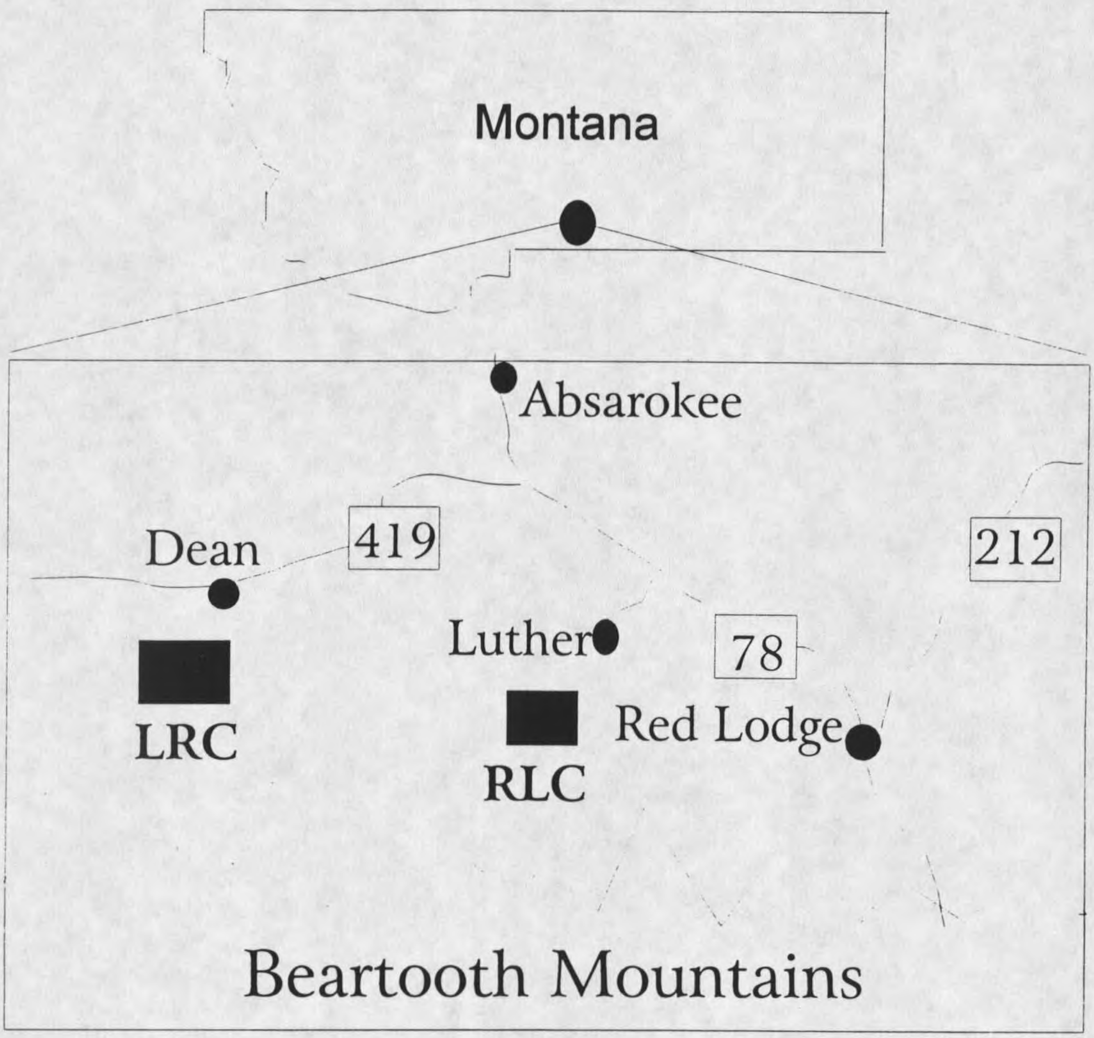

Figure 1. Location of Red Lodge Creek and Little Rocky Creek study sites at Luther and Dean, Montana, 1996-1998.

Using Geographic Information System maps of vegetative cover, five dominant forest cover types, aspen, conifer, mixed, broadleaf shrub, and meadow/grass, were identified in RLC.

The LRC drainage was located 51 km west of Red Lodge, Montana. LRC was 11.19 km^2, with elevation ranging from 1,860 m to 2,050 m, and had a very similar distribution of vegetation, both spatially and structurally to that in RLC. The same forest cover types were identified as in RLC based on these methods.

METHODS

Productivity

Capture and Marking

During 1996 and 1997, I trapped ruffed grouse each fall from late August through October and in the spring from late April to late May using cloverleaf walk-in traps (Dorney and Mattison 1956). I placed traps in presumed travel corridors and in observed high-use areas. Captured birds were weighed; aged (juvenile [<1year of age] or adult [>1year of age]) based on wear of outer primaries (Davis 1969); and sexed based on terminal tail band, length of central rectrices, eyebrow pigment, and presence of rump spots (Gullion 1989). Each bird was marked with 2 color-coded and numbered plastic leg bands (females right leg and males left leg) and a numbered aluminum Montana Fish Wildlife and Parks (MFWP) reward band (females left leg and males right leg). I fitted each female with a necklace-style radio transmitter (10.0 gm, 12-hour mortality sensor, 180 day battery). Each radio deployed during the fall automatically shut down for 240 days following initial activation to conserve battery life over the winter months.

Nest Data

During the nesting season, I attempted to locate each female every other day until her nest-site location was determined. I used a 3-element hand-held Yagi antenna to locate females via homing (Mech 1983). If a mortality sensor was activated, I immediately located the radio to determine the bird's status. Early in the nesting season I attempted to determine each females location within (40 m) every other day. When the location of a female was the same on two consecutive telemetry sessions, I assumed she was nesting and homed to within approximately 20 m of the female to estimate the location of her presumed nest. I continued to monitor each female presumed to be nesting for 14 days, at which time I flushed the female, located her nest site, and counted the eggs in the nest bowl. Each nest was then monitored every other day from distances that prevented flushing the hen until hatch date. If a hen was found off of her nest during the incubation period, the nest was examined for depredation, and the eggs were re-counted.

For each nest, I recorded clutch size, number of chicks that hatched, estimated nest- initiation date, actual hatch date for successful hens, estimated hatch dates for unsuccessful hens, and nest location. The number of chicks hatched from each nest was determined by examining nest bowls for egg caps and unhatched eggs within 24 hours of hatching. Nest-initiation dates were estimated by back-dating using clutch size and hatch date for successful hens. I backdated by assuming that a female laid an egg every 1.5 days and that incubation began on the day the last egg was laid and lasted 24 days (Bump et al. 1947). Clutch size at time of female death or nest destruction was used to estimate initiation dates for unsuccessful nests.

Brood Data

After a females brood hatched, I located the brood twice each week. To ascertain brood locations, I used telemetry to home within 20 m of a brood (based on signal strength). Once I was within 20 m of brood, an assistant and I slowly moving in opposite directions circled the brood and decreased our radius at every half circle until the exact location of the brood was determined. I considered the location of the first bird seen to be the brood location. This method reduced the potential for observer- induced movements. However, if I felt a brood's location was affected by observer activity, I discarded the observation and the brood was relocated two days later to ensure unbiased observations.

Each brood was radio-tracked for 49 days. Although broods were still acting as a unit up to and after day 49, individuals within broods were becoming more diffuse, often being flushed >20 m from each other by 49 days of age. This made accurate determination of their locations and number of individuals per brood impossible.

Survival Data

Survival data were obtained for radio-marked hens and their nests, broods, and chicks. Hen survival was the proportion of radio-marked females that survived from 1 May to 23 August. Hen success was the proportion of hens that hatched a nest. Nesting success was the proportion of nests that had at least one egg hatch. A brood was considered successful if it had at least one chick survive to 49 days. Chick survival was the proportion of chicks that survived to 49 days. Data on chick survival were obtained by counting the number of chicks in each brood at least once a week. When possible, counts were made without flushing hens and chicks in an attempt to minimize brood disturbance. However, due to dense habitat often used by broods, flushing was often required to get an accurate count of chicks. I flushed broods no more than once a week. I obtained a final count of chicks in each brood at 49 days of age to determine chick survival. I assumed that all surviving chicks remained with the hen to this age.

Following the 1997 nesting season it was apparent that estimates of nesting success would be negatively affected by the small sample sizes that I was obtaining for my study population. I therefore initiated an artificial-nest study in 1998 that had controllable sample sizes. I placed nests in two habitat types: 21 in conifer, 42 in aspen. Aspen stands in the two study areas were identified and numbered. I then chose 42 stands at random. Each nest site was determined by proceeding from the estimated center of a chosen aspen stand along a randomly chosen compass bearing. Each nest was >10 m from the edge of the respective habitat type because my objective was to estimate nesting success within each habitat type rather than at habitat edges. If the chosen location was <10 m from the edge, I randomly chose a different distance and a different compass bearing until the nest site was located $\geq$ 10 m from the edge. Nest sites in conifer stands were established by traveling from the forest boundary to randomly selected distances along the main forest roads and then proceeding perpendicular to the road at previously selected distances. Each nest was marked with a 4-cm^2 strip of flagging tape held in place at the nest bowl with a nail driven into the ground. Markers were concealed during placement of the eggs in the nest bowl. Each nest location was also marked with a piece of flagging at the edge of the stand. I recorded the compass bearing and distance to the nest on the flagging. Flags were $\geq$15 m from nest to reduce advertisement of nests to predators (Major and Kendall 1996). All artificial nests were $\geq$500 m from known nest sites of radio-marked hens to avoid potential attraction of nest predators.

Each artificial nest contained 1 small brown chicken egg and 1 clay egg placed in a scrape on the ground simulating a grouse nest. Plastic gloves were worn when building scrapes and placing eggs in nests. Artificial nests were checked every 5 days over a 3-week period for evidence of predation. A nest was considered to be depredated if eggs were moved, missing or broken or if clay eggs had imprints left by predators. The type of disturbance to eggs and the nature of imprints left in clay eggs were used to help identify predators (Hannon and Cotterill 1998).

Nesting success rates for artificial nests were calculated based on 2 predation criteria: (1) predation resulting in missing or moved eggs, crushed eggs, or teeth marks in clay eggs from large mammals (Vulpes fulva, Mephitis mephitis etc.) or bill marks from avian predators, and (2) any sign of predation, including teeth marks in clay eggs from small mammals. The two predation criteria were used to differentiate between predation by avian predators and larger mammals that grouse hens would likely not be able to defend against and predation from any source, including small mammals, some of which grouse hens would likely be able to defend against. I believe that predation criteria 2 over estimated predation and underestimated nesting success by assuming the appearance of small mammal teeth marks in clay eggs would automatically result in an unsuccessful nest. Therefore, analyses, results, and discussion of artificial nesting in this paper will be based on estimates using predation criteria 1. Nesting success results based on predation criteria 2 are available in appendix A for referral.

Habitat Selection

Nest Habitat

I collected habitat data at each nest sites 0 to 4 days after actual (successful nests) or expected (unsuccessful nests) hatch date. For micro-habitat measurements (see appendix B for conversion of micro-habitat measurements from metric to English units), I used a circular plot (8.5 m in diameter), centered on the nest bowl and measured the following: canopy cover; percent ground cover by shrub, grass, forb, and downed woody debris; number of snags by height and basal diameter class; trees by species, height and basal diameter class; and shrubs by species and basal diameter class. Canopy cover was the average estimates in the 4 cardinal directions taken at the nest bowl using a spherical densiometer. Percent ground cover was estimated by placing a 0.5^2 m square frame 2.5 m from the nest bowl in all cardinal directions, making ocular estimates of the percent ground cover within each square, and then averaging these estimates. Snags and trees were divided into 4 height classes (0.5 m - 3 m, >3 m -10 m, >10 m - 30 m, >30 m) and 6 basal diameter classes (2 cm - 10 cm, >10 cm - 20 cm, >20 cm - 30 cm, >30 cm - 50 cm, >50 cm - 70 cm, >70 cm). Shrubs were divided into 6 basal diameter classes (0.5 cm - 1 cm, >1 cm - 2 cm, >2 cm - 3 cm, >3 cm - 4 cm, >4 cm - 6 cm, >6 cm).

I also measured the following macro-habitat variables: distance to nearest aspen; distance to water; and distance to clearing (clearing being defined as an area $\geq$ 8.5 m circle with $\leq$15% canopy cover). Distance to aspen was estimated by pacing. Distance to water was estimated by either pacing or use of topographical maps. Distance to clearing was estimated by pacing and using densiometer procedures described above.

Brood Habitat

I collected habitat data for each brood site that I identified via telemetry. When broods were flushed during location estimation, habitat data were collected immediately. When broods were not flushed during location estimation, I marked the location and returned within 4 days to record the brood habitat data. This method was employed to minimize the impact that I had on brood locations during collection of data. For micro-habitat measurements, I used a circular plot (8.5 m in diameter) centered on the location where the first bird was observed in the brood. Canopy cover was estimated at 2.5 m in all cardinal directions from the plot center and then averaged to better represent the site used by the entire brood. All other habitat variables and data collection methods were the same as those used for nest plots (see above).

Random Sites

I also collected habitat data on 50 sites randomly selected from the entire study area (25 in each study site) from 1 June to 30 July. Random sites were centered on randomly selected UTM coordinates. Canopy cover was estimated at both the center of the plot (as in nest plots) and at 2.5 m from plot center (as in brood plots). Plot size and all other habitat variables and data collection methods were the same as for nest and brood plots.

DATA ANALYSIS

Productivity

Nest Data

I used t-tests to compare nest-initiation dates between years and between successful and unsuccessful nests and to compare clutch sizes between years. I used chi-square analysis (Yates corrected) to test for differences in hen survival and hen success between years. I also used chi-square analysis (Yates corrected) to test for differences in nest success between years and between aspen and conifer stands. I also used chi-square analysis (Yates corrected) to test for differences in nest success between natural and artificial nests in all habitats and within aspen and conifer.

Brood Data

I used chi-square analysis (Yate's corrected) to compare annual brood survival rates. I used t-tests to compare chick survival between years. Since fates of broodmates were likely not independent, I calculated chick survival for each brood and used these estimates to estimate chick survival. Therefore, the sample size for estimating chick survival equals the number of broods.

Habitat Selection

Nest Data

I used the method of Marcum and Loftsgarden (1980) on data for forest cover type at used and available nest sites to test for habitat selection during nesting. I also used a combination of univariate and multivariate analyses to evaluate differences between habitat at nest sites and random sites. Due to small sample sizes and absence of confounding effects of vegetation structure and composition between years, I combined data from 1997 and 1998.

For univariate analyses, I used a t-test to compare each habitat variable between: (1) successful and unsuccessful nest sites and (2) nest sites and random sites. Habitat variables were divided into micro-habitat and macro-habitat categories. Twelve variables were compared in the micro-habitat analysis, and 3 variables were compared in the macro-habitat analysis. However, because univariate analysis of this type involves conducting multiple tests on data from the same set of nests and random plots, I used Rice's (1990) sequential Bonferroni correction when evaluating the significance of results.

Multivariate analysis of habitat use was examined using logistic regression. A variable was a candidate in the logistic-regression model if the univariate analysis of site type versus that variable was significant at $\underline{P} < 0.25$. A conservative significance level was chosen to prevent elimination of variables that may have been important to productivity when examined together (Hosmer and Lemeshow 1989). Candidate variables were entered into logistic regression and evaluated using maximum likelihood estimation. This produced log-likelihood values for each model that measured the discrepancy of the fit between the data and the model (Burnham and Anderson 1992). These values were adjusted using Akaike's information criterion (AIC)(Burnham and Anderson 1992). The best model was then chosen based on the smallest AIC value. AIC values provide an evaluation of model fit, emphasize parsimony, and have been suggested for selection among models in a likelihood context (Burnham and Anderson 1992). All models whose AIC values were within two units of the AIC value of the most parsimonious model were considered part of a confidence list of models and evaluated (Burnham and Anderson 1992). For each model, I also calculated the P-value associated with a likelihood ratio test comparing the estimated model to the null model and a logistic regression R^2 value that measured the proportion of the model's log-likelihood that was explained by the fitted model. To ensure precision and avoid mainly spurious correlations when model building (Burham and Anderson 1998), it is recommended that the amount of observations be at least 6-20 times the number of variables collected (StatSoft inc. 1994, Neter et al.1996). Because the number of observations in this study did not permit examining micro-habitat and macro-habitat variables combined based on published modeling recommendations, separate models were developed for micro-habitat variables and for macro-habitat variables.

Model construction incorporated both a priori and a posteriori components. Explanatory variables used for model building were determined a priori based on scientific literature. However, because my study area differed structurally and regionally from most published research addressing ruffed grouse ecology, I did not feel confident in identifying a priori models as suggested by Burnham and Anderson (1998). Therefore, a posteriori models containing all possible combinations of explanatory variables were constructed and evaluated. Thus, this analysis was exploratory rather than confirmatory and the results should be treated as potential hypotheses to be tested in future research (Burnham and Anderson 1998).

<u>Brood Data</u>

I used the method of Marcum and Loftsgarden (1980) on data for forest cover type at used and available brood locations to test for habitat selection during brood rearing. I also used a combination of univariate and multivariate analysis to compare habitat between brood sites and random sites, and between broods experiencing different levels of chick survival. A t-test was used to compare each habitat variable among brood and random sites, and between broods experiencing different levels of chick survival. Twelve variables were used in the micro-habitat analysis, and 3 variables were used for the macro-habitat analysis. Rice's sequential Bonferroni correction (Rice 1990) was used when evaluating significance of results. Multivariate analysis techniques examining brood site selection and habitat used by broods experiencing different levels of chick survival were the same as those described for nest data.

I analyzed chick survival (lived or died status for each chick) versus the proportion of time that each brood was estimated to be in aspen, conifer, or mixed cover types using logistic regression. Because other studies have reported mortality rates for chicks to be age dependent (Bump et al. 1947; Kupa 1966), analysis of chick survival based solely on cover type without examining age effects may produce biologically misleading results. Therefore, 2 age-specific variables (age in weeks and a dummy variable distinguishing chicks <1 week old from older chicks), 3 cover-type variables (proportion of brood locations in aspen, conifer, and mixed forests) and 3 interaction terms were included in this analysis to estimate the effect of cover type on chick survival. These variables were entered into logistic regression and log-likelihood values were produced for each model. These values were then adjusted using AIC_c, which is an AIC adjusted for small sample size (Burnham and Anderson 1998). However, the biology of ruffed grouse broods indicates that fates of broodmates are likely not independent. Ruffed grouse broods live as a coherent unit after hatching in the spring until sometime in early autumn when brood break-up and dispersal commences (Godfrey and Marshall 1969). Members of such groups often lack independence of individual responses (Burnham and Anderson 1998). Violations of the independence assumption often cause count data to be over dispersed (sampling variance exceeds model based variance)(Burnham and Anderson 1998). To correct for this overdispersion, an overdispersion factor of 3 was applied to all models AIC_c values, creating Quasi-likelihood values ($QAIC_c$)(Burnham and Anderson 1998). An overdispersion factor of 3 was used because overdispersion due to violations of independence usually range from just above 1 to approximately 4 (Burnham and Anderson 1998). Models were then selected based on $QAIC_c$ values. All models whose $QAIC_c$ values were within two units of the $QAIC_c$ value of the most parsimonious model were considered part of a confidence list of models and evaluated (Burnham and Anderson 1992).

Given the sample sizes in this study, the level of significance for all statistical tests was set at 0.1 to achieve a better balance between Type 1 and Type 2 statistical errors (Steel and Torrie 1980). Analysis of chick survival based on cover type use and age was conducted using program MARK (White, no date). All other analyses were conducted using program STATISTICA (StatSoft, Inc. 1994).

RESULTS

Productivity

Capture and Marking

In the fall of 1996, 8 females and 21 males were captured in 365 trap days. Of these 8 females, 2 were killed during hunting season, 1 carried a faulty radio, 3 died overwinter, and only 2 survived to nest initiation. In the spring of 1997, 5 females and 11 males were captured in 443 trap days. All 5 of these females survived to nest initiation. Thus 7 females were monitored during the 1997 nesting season. In the fall of 1997, 2 females and 7 males were captured in 353 trap days. Both females died overwinter. In the spring of 1998, 1 female and 6 males were captured in 263 trap days. This female survived to nest initiation. Also, 3 hens captured in the spring of 1997 still had functioning radios on 1 May 1998. Two of these females survived to nest initiation in 1998. Thus 3 females were monitored during the 1998 nesting season (Table 1).

Nest Data

I located 12 nests, which included nests from 8 different females and what I believed to be 10 initial nest attempts and 2 renest attempts (Table 2). Mean nest initiation date for initial nesting attempt was 17 May in 1997 (SE = 1.28) and in 1998 (SE = 7.68). Two renest attempts were initiated (one on 9 June and one on 14 June), 8 and 9 days, respectively, after depredation or abandonment of

Table 1. Annual ruffed grouse trapping results at Luther and Dean, Montana, 1996-1998.

Year/Season	Trap days	Total birds captured	Males captured	Females captured	# of females that survived to breeding	# of females that nested	# of females that had broods
1996/Fall	365	29	21	8	2[a]	2	1[b]
1997/Spring	443	16	11	5	5[a]	5	3[b]
1997/Fall	353	9	7	2	0	0	0
1998/Spring	263	7	6	1	1	1	1
Total	1424	61	45	16	8	8	5

[a] One female trapped in 1996 Fall and 1 female trapped in 1997 Spring survived to breeding season in 1997 and 1998.

[b] Both females that survived to two breeding seasons failed to produce broods in 1997, but did produce broods in 1998.

Table 2. Annual ruffed grouse nesting data at Luther and Dean, Montana, 1997-1998.

Year	Hens	Nests	Renest	Initiation Date[a]		Nest Success[b]		Hatch Date		Clutch Size	
				Mean	SE	Mean	SE	Mean	SE	Mean	SE
1997	7	7	2	17 May	1.28	0.22[c]	0.20	22 June	0.50	9.50[d]	0.50
1998	3	3	0	17 May	7.68	1.00	0.00	25 June	5.89	10.00	1.53
Total	8[e]	10[f]	2	17 May	2.17	0.42	0.15	23 June	3.31	9.75	0.86

[a] Mean initiation for first nest attempt. Estimated by assuming 3 days to lay 2 eggs and 24-day incubation period.
[b] Mean probability that a nest will hatch $\geq$ 1 egg. Includes initial and renest attempts.
[c] X^2 indicated an annual difference ($\underline{P}$ = 0.09).
[d] T-test did not indicate an annual difference ($\underline{P}$ = 0.82).
[e] Two females initiated nests in both 1997 and 1998.
[f] Eight hens were responsible for the 10 nest attempts and the 2 renests.

original nests. Both renest attempts were in different habitat types than the original attempts and both were unsuccessful.

Nest success over the two-year period was 0.42 (SE = 0.15) and was greater (P = 0.09) in 1998 (mean = 1.00, SE = 0.00) than in 1997 (mean = 0.22, SE = 0.20). Nest success did not differ (P = 0.68) between aspen/hardwood (mean = 0.33, SE = 0.21) and conifer (mean = 0.40, SE = 0.24) during the study (Table 3). The initiation date of first nests was not related to nest success (P = 0.73).

Hen success was 0.50 (SE = 0.16) over the 2 year period and was not significantly different (P = 0.17) between 1997 (mean = 0.28, SE = 0.18) and 1998 (mean = 1.00, SE = 0.00). Hen survival from May through August averaged 0.72 (SE = 0.13) and did not differ (P = 0.89) between 1997 (mean = 0.71, SE = 0.48) and 1998 (mean = 0.75, SE = 0.50). Two females died while nesting in 1997 and 1 died prior to nesting in 1998. All females survived during brood-rearing in each year.

The earliest hatch dates were 22 June in 1997 and 18 June in 1998. The average hatch date over the two year period was 24 June (SE = 3.31). In successful nests, 89% of 19 eggs hatched in 1997, and 93% of 30 eggs hatched in 1998 (mean = 92%, n = 5 nests).

Overall artificial-nest success was 0.72 (SE = 0.06), which was greater than natural-nest success (P = 0.06)(Table 3.). Artificial-nest success was greater in aspen stands (P = 0.06)(mean = 0.83, SE = 0.38) than in conifer stands (mean = 0.52, SE = 0.11). Artificial-nest success in aspen was greater than natural nest

Table 3. Ruffed grouse nesting success in aspen and conifer cover types in Luther and Dean, Montana, 1997-1998.

	Nest Type					
	Natural[a]			Artificial[b]		
Habitat Type	Nests(n)	Mean	SE	Nests(n)	Mean	SE
Aspen[c]	6	0.33	0.21	41	0.83[d]	0.38
Conifer[e]	5	0.40	0.24	21	0.52	0.11
Total[fg]	12	0.42	0.15	62	0.72	0.06

[a] Proportion of nests that hatched at least one chick in 1997 and 1998.
[b] Proportion of nests in which neither egg was moved, missing, crushed, or the clay had no visible signs of predation from large mammals or avian predators. All nests from 1998.
[c] X^2 indicated a significant difference ($\underline{P}$ = 0.03) between artificial nest success in aspen and natural nest success in aspen.
[d] X^2 indicated a significant difference ($\underline{P}$ = 0.06) between artificial nest success in aspen and artificial nest success in conifer.
[e] X^2 indicated no significant difference ($\underline{P}$ = 0.85) between artificial nest success in conifer and natural nest success in conifer.
[f] X^2 indicated a significant difference ($\underline{P}$ = 0.06) between overall artificial nest success and overall natural nest success.
[g] The natural nests used to compare overall natural nest success to overall artificial nest success consisted of 5 nests in aspen, 6 nests in conifer, and 1 nest in mixed hardwood/conifer cover type.

success in aspen ($\underline{P}$ = 0.03). Artificial-nest success in conifer did not differ from natural-nest success in conifer ($\underline{P}$ = 0.85).

Brood Data

Data were collected on 5 broods from 5 different females (2 broods in 1997 and 3 in 1998). Mean brood size at hatching was 9.0 (SE = 1.05)(Table 4) and did not differ ($\underline{P}$ = 0.61) between 1997 (mean = 8.50, SE = 1.50) and 1998 (mean = 9.33, SE = 1.05) . All broods produced at least 1 49-day-old chick. The chick survival probability over the 2 year period was 0.37 (SE = 0.03) and did not differ ($\underline{P}$ = 0.35) between 1997 (mean = 0.49, SE = 0.20) and 1998 (mean = 0.29, SE = 0.03).

Habitat Selection

Nest Habitat

I collected habitat data for 12 nest sites and 50 random sites during 1997-1998. Over the 2 nesting seasons females nested in aspen cover types more than expected, meadow/grass cover types less than expected and conifer, mixed, and shrub cover types in proportion to their availability (overall X^2 = 8.32, $\underline{P}$ = 0.08)(Table 5). Most birds (83%) nested at the base of a tree or log. However, one bird nested 7 m from the closest natural nest backstop in fairly open terrain at the bottom of an intermittent stream and a second bird nested in

Table 4. Survival of ruffed grouse broods and chicks in Luther and Dean, Montana, 1997-1998.

Year	Broods	Brood Size[a]		Brood Survival[b]		Chick Survival[c]		Chicks Alive at day 49	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
1997	2	8.50[d]	1.50	1.00	0.00	0.49[e]	0.20	4.50	2.50
1998	3	9.33	2.88	1.00	0.00	0.29	0.07	2.55	0.33
Total	5	9.00	1.05	1.00	0.00	0.37	0.03	3.50	0.93

[a] Average number of chicks hatched per brood.
[b] Mean probability of a brood producing $\geq$ 1 49 -day -old chick.
[c] Mean probability of chicks alive per brood at day 49 after hatch.
[d] T-test indicated no difference ($\underline{P} = 0.61$) between years.
[e] T-test indicated no difference ($\underline{P} = 0.35$) between years.

Table 5. Analyses of forest-cover-type selection for nesting ruffed grouse at Luther and Dean, Montana, 1997-1998.

Forest Cover Type	Nest Locations n	Nest Locations %	Random Locations n	Random Locations %	Habitat Use	90% Simultaneous CI's[a] used to estimate habitat use versus availability
Aspen	6	50	7	14	more than expected	-0.71 to -0.01
Conifer	5	42	33	66	in proportion to availability	-0.13 to 0.60
Mixed	1	08	4	08	in proportion to availability	-0.20 to 0.20
Meadow/Grass	0	00	5	10	less than expected	0.09 to 0.10
Broadleaf Shrub	0	00	1	02	in proportion to availability	-0.02 to 0.06

[a] Marcum and Loftsgarden (1980) analysis of habitat selection. If the confidence interval includes 0, that cover type is used in proportion to its availability. If both end points of the interval are positive, that forest cover type is used less than expected based on its availability. If both end points of the interval are negative, that cover type is used more than expected based on in its availability.

a grove of ninebark with no obvious nest backstop. Three birds that nested in aspen or mixed hardwood cover types chose to nest under Englemann spruce.

Univariate Analysis Univariate analysis indicated no differences between micro-habitat variables at successful and unsuccessful nest sites (Table 6). Univariate analysis of micro-habitat variables at nest sites and random sites indicate that stem densities of cottonwood species were greater ($\underline{P} < 0.01$) at nest sites (mean = 1.25, SE = 0.82) than at random sites (mean = 0.08, SE = 0.04)(Table 7).

Univariate analysis of macro-habitat variables indicated no differences between variables at successful and unsuccessful nests (Table 8) or between variables at nest sites and random sites (Table 9).

Multivariate Analysis The most parsimonious model produced by logistic regression for comparisons of successful and unsuccessful nest sites at the micro-site level contained percent canopy cover and stem densities of Englemann spruce (Table 10). This model was more parsimonious than the null model (Δ AIC 3.256) and had a logistic regression R^2 value of 0.59. Logistic regression indicated that there was greater canopy cover and reduced stem densities of Englemann spruce at successful nests than at unsuccessful nests. No macro-habitat explanatory variables were entered into a multiple logistic regression.

The most parsimonious model produced by logistic regression for comparison of nest sites and random sites at the micro-habitat level included cottonwood species stem densities, shrub stem densities, and percent canopy cover

Table 6. Results of univariate comparisons of micro-habitat characteristics at successful and unsuccessful ruffed grouse nest at Luther and Dean, Montana, 1997- 1998.

Habitat Variable[a]	Successful Nests (n = 5) Mean	SE	Unsuccessful Nests (n = 7) Mean	SE	Observed P[b]	Critical P[c]
CC	87.26	4.60	71.14	9.88	0.22	0.01
GC	45.90	10.87	42.17	7.53	0.77	0.10
SHR	576.80	142.90	439.28	112.30	0.46	0.02
SHRDV	7.60	1.07	8.14	0.55	0.64	0.05
SNG	12.40	4.82	6.71	2.08	0.25	0.01
TR	43.40	17.37	29.14	8.14	0.43	0.02
PSME	4.40	2.76	6.85	3.21	0.59	0.03
PICO	10.60	9.86	5.57	3.61	0.59	0.03
POTR	27.40	18.23	9.85	6.23	0.32	0.01
PIEN	0.40	0.40	3.14	1.83	0.24	0.01
POPSPP	0.20	0.20	2.00	1.36	0.29	0.01
CONSPP	0.00	0.00	1.71	1.39	0.33	0.01

[a] CC= % overhead canopy cover; GC= % ground cover composed of shrubs, forbs, grass, and downed woody debris; SHR= # of shrub stems/plot >.4cm basal diameter; SHRDV= shrub diversity; SNG= # of snags > 2cm basal diameter and > .5m in height; TR= # of trees > 2cm basal diameter and > .5m in height; PSME=# of Douglas fir > 2cm basal diameter and > .5m in height; PICO= # of Lodgepole pine >2cm basal diameter and > .5m in height; POTR= # of Quaking aspen > 2cm basal diameter and > .5m in height; PIEN= # of Englemenn spruce > 2cm basal diameter and > .5m in height; POPSPP= # of trees of Cottonwood spp. > 2cm basal diameter and > .5m in height; CONSPP= # of trees of other

Table 6. (continued)

conifer species (Abies lasiocarpa, Pinus flexilus, Pinus ponderosa, Pinus albicaulus) > 2cm basal diameter and > .5m in height. Species included in this variable were found on <10% of all sites.

[b] Observed significance level of T-test.

[c] Since 12 variables measured on the same plots were used to test for differences, Rice's sequential Bonferroni correction to assess significance of results was employed. This procedure involves: 1) ranking the set of P-values from smallest to largest, 2) determining if the smallest P-value is less than the Rice's adjusted P (i.e. $P_1 \leq [1-(1-0.1)^{1/k}]$ where k=number of variables, 3) and if this condition is met continue by using $P_j \leq [1-(1-0.1)^{1/k-j}$ where j = rank of variable, until the inequality is met or all P-values have been evaluated. Observed significance levels must be less than adjusted levels to achieve significance at the 0.1 level.

Table 7. Results of univariate comparison of micro-habitat characteristics at ruffed grouse nest sites and random sites at Luther and Dean, Montana, 1997-1998.

Habitat	Nest Sites (n = 12)		Random Sites (n = 50)		Observed	Critical
Variable[a]	Mean	SE	Mean	SE	P[b]	P[c]
CC	77.85	6.32	62.48	5.04	0.16	0.01
GC	43.72	6.02	36.61	3.35	0.34	0.01
SHR	496.58	86.74	349.84	34.54	0.08	0.01
SHRDV	7.91	0.52	6.34	0.39	0.07	0.01
SNG	9.08	2.37	10.56	1.77	0.70	0.03
TR	35.08	8.44	31.68	3.97	0.71	0.03
PSME	5.83	2.14	6.22	1.77	0.92	0.10
PICO	7.66	4.41	14.76	4.14	0.42	0.02
POTR	17.16	8.33	5.72	1.81	0.04	0.01
PIEN	2.00	1.12	2.20	0.77	0.91	0.05
POPSPP	1.25	0.82	0.08	0.04	<0.01[d]	0.01
CONSPP	1.00	0.82	2.02	0.83	0.56	0.02

[a] CC= % overhead canopy cover; GC= % ground cover composed of shrubs, forbs, grass, and downed woody debris; SHR= # of shrub stems/plot >.4cm basal diameter; SHRDV= shrub diversity; SNG= # of snags > 2cm basal diameter and > .5m in height; TR= # of trees > 2cm basal diameter and > .5m

Table 7. (continued)

in height; PSME=# of Douglas fir > 2cm basal diameter and > .5m in height; PICO= # of Lodgepole pine >2cm basal diameter and > .5m in height; POTR= # of Quaking aspen > 2cm basal diameter and > .5m in height; PIEN= # of Englemenn spruce > 2cm basal diameter and > .5m in height; POPSPP= # of trees of Cottonwood spp. > 2cm basal diameter and > .5m in height; CONSPP= # of trees of other conifer species (Abies lasiocarpa, Pinus flexilus, Pinus ponderosa, Pinus albicaulus) > 2cm basal diameter and > .5m in height. Species included in this variable were found on <10% of all sites.

[b] Observed significance level of T-test.

[c] Since 12 variables measured on the same plots were used to test for differences, Rice's sequential Bonferroni correction to assess significance of results was employed. This procedure involves: 1) ranking the set of P-values from smallest to largest, 2) determining if the smallest P-value is less than the Rice's adjusted P (i.e. $P_1 \leq [1-(1-0.1)^{1/k}]$ where k=number of variables, 3) and if this condition is met continue by using $P_j \leq [1-(1-0.1)^{1/k-j}$ where j = rank of variable, until the inequality is met or all P-values have been evaluated.

[d] P-values that were significant following Rices's sequential Bonferroni correction.

Table 8. Results of univariate comparisons of macro-habitat characteristics at successful and unsuccessful ruffed grouse nests at Luther and Dean, Montana, 1997-1998.

Habitat	Successful Nests (n = 5)		Unsuccessful Nests (n = 7)		Observed	Critical
Variable[a]	Mean	SE	Mean	SE	P[b]	P[c]
DPOTR	47.95	40.77	10.55	5.07	0.30	0.03
DC	29.40	15.16	22.90	13.07	0.76	0.10
DH2O	86.69	41.43	148.59	49.95	0.39	0.05

[a] DPOTR = Distance to nearest aspen; DC = Distance to clearing (clearing is defined as an area with overhead canopy <15%); DH2O = Distance to any standing body of water.

[b] Observed significance level of T-test.

[c] Since 3 variables measured on the same plots were used to test for differences, Rice's sequential Bonferroni correction to assess significance of results was employed. This procedure involves: 1) ranking the set of P-values from smallest to largest, 2) determining if the smallest P-value is less than the Rice's adjusted P(i.e. $P_1 \leq [1-(1-0.1)^{1/k}]$ where k=number of variables, 3) and if this condition is met continue by using $P_j \leq [1-(1-0.1)^{1/k-j}$ where j = rank of variable, until the inequality is met or all P-values have been evaluated. Observed significance levels must be less than adjusted levels to achieve significance at the 0.1 level.

Table 9. Results of univariate comparisons of macro-habitat characteristics at ruffed grouse nest sites and random sites at Luther and Dean, Montana, 1997-1998.

Habitat	Nest Site ($\underline{n}$ = 12)		Random Site ($\underline{n}$ = 50)		Observed	Critical
Variable[a]	Mean	SE	Mean	SE	P[b]	P[c]
DPOTR	26.10	17.05	55.57	10.47	0.20	0.05
DC	25.66	9.47	38.77	8.54	0.47	0.10
DH2O	122.79	33.73	212.02	24.08	0.09	0.03

[a] DPOTR = Distance to nearest aspen; DC = Distance to clearing. In this study clearing is defined as an area with overhead canopy <15%; DH2O = Distance to any standing body of water.

[b] Observed significance level of T-test.

[c] Since 3 variables measured on the same plots were used to test for differences, Rice's sequential Bonferroni correction to assess significance of results was employed. This procedure involves: 1) ranking the set of P-values from smallest to largest, 2) determining if the smallest P-value is less than the Rice's adjusted P(i.e. $P_1 \leq [1 -(1-0.1)^{1/k}]$ where k=number of variables, 3) and if this condition is met continue by using $P_j \leq [1-(1-0.1)^{1/k-j}$ where j = rank of variable, until the inequality ismet or all P-values have been evaluated. Observed significance levels must be less than adjusted levels to achieve significance at the 0.1 level.

Table 10. Multiple logistic regression models of micro-habitat and macro-habitat variables predicting the probability of ruffed grouse nest success at Luther and Dean, Montana, 1997-1998.

		Model Evaluation[b]			
Model Type	logit [a]	AIC	Δ AIC	R^2	P
Micro.[c]	-6.53 + 0.08(CC) - 0.47(PIEN)	15.04	0.00	0.59	0.07
Null[e]	-0.34	18.30	3.26	<0.01	
Macro.[d]	No variables entered model				

[a] Logit of the equation estimating the probability of a nest site being successful. Variables with positive coefficients are positively related to a nests probability of success.
[b] Model evaluation parameters are: Akaike's Information Criterion (AIC) which is used to select the most parsimonious model; Δ AIC which shows differences in AIC values among models; R^2 measures the proportion of the model's log-likelihood explained by the model; P value is associated with a likelihood ratio test comparing the estimated model to the null model. All models with an AIC value within 2 units of the AIC value for the most parsimonious model were evaluated.
[c] Micro-habitat variable analysis.
[d] Macro-habitat variable analysis.
[e] Null is a model with an intercept term only.

(Table 11). This model was more parsimonious than the null model (Δ AIC 10.23) and had an R^2 value of 0.53. Logistic regression indicated that nest sites had greater stem densities of cottonwood species and shrub, and had greater canopy cover than random sites. Two other models were within 2 AIC units of the most parsimonious model and were included in the confidence list of models. Cottonwood species stem density and shrub stem density were included in all 3 models and the signs associated with coefficients for each variable remained consistent across all models. Percent canopy cover and aspen stem density appeared in 2 and 1 models respectively, and both were positively correlated with nest-site selection.

The most parsimonious model produced by logistic regression for comparison of nest sites and random sites at the macro-habitat level included distance to nearest aspen stand and distance to nearest water. Although this model was more parsimonious than the null model (Δ AIC 4.11), a likelihood-ratio test did not indicate a better fit to the data than the null model ($\underline{P} = 0.13$).

Brood Habitat

I collected data from 5 broods, at 74 brood site locations during 1997-1998. Over the two-year period, broods used aspen and mixed cover types more than expected, conifer and meadow/grass cover types less than expected, and broadleaf shrub cover types in proportion to their availability (overall $X^2 = 49.84$, $\underline{P} < 0.01$)(Table 12).

Table 11. Multiple logistic regression models of micro-habitat and macro-habitat variables predicting the probability of ruffed grouse nest site selection in Luther and Dean, Montana, 1997-1998.

Model Type	logit[a]	Model Evaluation[b] AIC	Δ AIC	R^2	P
Micro.[c]	-4.91 + 1.057(POPSPP) + 0.003(SHR) + 0.026(CC)	52.69[f]	0.00	0.53	<0.01
	-2.92 + 0.972(POPSPP) + 0.003(SHR)	54.08	1.39	0.47	<0.01
	-4.76 + 1.070(POPSPP) + 0.003(SHR) + 0.025(CC) + 0.012(POTR)	54.42	1.73	0.54	0.01
Null[d]	-1.47	62.92	10.23	<0.01	
Macro[e]	-0.648 - 0.006(DPOTR) - 0.003(DH2O)	58.81[g]	0.00	0.29	0.13[h]
Null[d]	-1.47	62.92	4.11	<0.01	

[a] Logit of the equation estimating the probability nest site selection. Variables with positive coefficients are positively related to a sites probability of being selected for nesting.

[b] Model evaluation parameters are: Akaike's Information Criterion (AIC) which is used to select the most parsimonious model; Δ AIC which shows differences in AIC values among models; R^2 measures the proportion of the model's log-likelihood explained by the model; P value is associated with a likelihood ratio test comparing the

Table11. (continued)

estimated model to the null model. All models with an AIC value within 2 units of the AIC value for the most parsimonious model were evaluated.

[c] Micro-habitat variable analysis.

[d] Null is a model with an intercept term only.

[e] Macro-habitat variable analysis.

[f] Most parsimonious model for micro-habitat variable analysis.

[g] Most parsimonious model for macro-habitat variable analysis.

[h] Estimated model does not yield a better fit to the data than the null model.

Table 12. Analyses of forest-cover-type selection for brood-rearing grouse at Luther and Dean, Montana, 1997-1998.

Forest Cover Type	Brood Locations n	Brood Locations %	Random Locations n	Random Locations %	Habitat Use	90% Simultaneous CI's[a] Used to estimate habitat use versus availability
Aspen	32	43	7	14	more than expected	-0.46 to -0.12
Conifer	11	15	33	66	less than expected	0.34 to 0.70
Mixed	26	35	4	8	more than expected	-0.43 to -0.11
Meadow/Grass	0	0	5	10	less than expected	0.01 to 0.19
Broadleaf Shrub	5	7	1	2	in proportion to availability	-0.11 to 0.03

[a] Marcum and Loftsgarden (1980) analysis of habitat selection. If the confidence interval includes 0, that cover type is used in proportion to its availability. If both end points of the interval are positive, that forest cover type is used less than based on its availability. If both end points of the interval are negative, that cover type is used greater than expected based on its availability.

Brood Site Selection

Univariate Analysis Univariate analysis of micro-habitat variables at brood sites and random sites indicated significant differences between site types for 5 variables (Table 13). Brood sites were characterized as having greater shrub ($\underline{P}$ < 0.01) and aspen-stem densities ($\underline{P}$ < 0.01), higher percentages of canopy ($\underline{P}$ < 0.01) and ground cover ($\underline{P}$ < 0.01), and lower stem densities of lodgepole pine ($\underline{P}$ < 0.01) than did random sites. Univariate analysis of macro-habitat variables at brood sites and random sites indicated that brood sites were located significantly closer to aspen stands ($\underline{P}$ < 0.01) and water ($\underline{P}$ < 0.01)(Table 14) than were random sites.

Multivariate Analysis The most parsimonious model produced by logistic regression for comparison of brood sites and random sites at the micro-site level included shrub stem density, percent canopy cover, percent ground cover, and lodgepole pine stem density (Table 15). This model was more parsimonious than the null model (Δ AIC 41.53) and had an R^2 value of 0.66. Logistic regression indicated that brood sites had reduced lodgepole pine stem densities, greater shrub stem densities and greater canopy and ground cover than did random sites. Two other models were within 2 AIC units of the most parsimonious model and were included in the confidence list of models. All models in the confidence list included shrub stem density, percent canopy cover and percent ground cover and the signs associated with coefficients for each variable were consistent across all models. One model also included aspen stem density which was positively correlated to brood-site selection.

Table 13. Results of univariate comparisons of micro-habitat variables at ruffed grouse brood sites and random sites at Luther and Dean, Montana, 1997-1998.

Habitat	Brood Sites (n = 74)		Random Sites (n = 50)		Observed	Critical
Variable[a]	Mean	SE	Mean	SE	P[b]	P[c]
CC	77.63	1.98	62.48	5.04	<0.01[d]	0.01
SNG	15.90	1.51	10.56	1.77	0.02	0.01
TR	33.09	4.08	31.68	3.97	0.81	0.10
PSME	3.04	0.98	6.22	1.77	0.09	0.03
PICO	2.42	0.75	14.76	4.14	<0.01[d]	0.01
POTR	20.98	3.91	5.72	1.81	<0.01[d]	0.01
PIEN	4.31	0.94	2.20	0.77	0.11	0.03
POPSPP	0.04	0.03	0.08	0.04	0.42	0.05
SHRDV	8.00	0.34	6.34	0.39	0.03	0.02
SHR	575.62	29.51	349.84	34.54	<0.01[d]	0.01
GC	46.86	2.10	36.61	3.35	<0.01[d]	0.01
CONSPP	0.47	0.18	2.02	0.83	0.03	0.02

[a] CC= % overhead canopy cover; GC= % ground cover composed of shrubs, forbs, grass, and downed woody debris; SHR= # of shrub stems/plot >.4cm basal diameter; SHRDV= shrub diversity; SNG= # of snags > 2cm basal diameter and > .5m in height; TR= # of trees > 2cm basal diameter and > .5m in height; PSME=# of Douglas fir > 2cm basal diameter and > .5m in height; PICO= # of Lodgepole pine >2cm basal diameter and > .5m in height; POTR= # of Quaking aspen > 2cm basal diameter and > .5m in height; PIEN= # of Englemenn spruce

Table 13. (continued)

> 2cm basal diameter and > .5m in height; POPSPP= # of trees of Cottonwood spp. > 2cm basal diameter and > .5m in height; CONSPP= # of trees of other conifer species (Abies lasiocarpa, Pinus flexilus, Pinus ponderosa, Pinus albicaulus) > 2cm basal diameter and > .5m in height. Species included in this variable were found on <10% of all sites.

[b] Observed significance level of T-test.

[c] Since 12 variables measured on the same plots were used to test for differences, Rice's sequential Bonferroni correction to assess significance of results was employed. This procedure involves: 1) ranking the set of P-values from smallest to largest, 2) determining if the smallest P-value is less than the Rice's adjusted P (i.e. $P_1 \leq [1-(1-0.1)^{1/k}]$ where k=number of variables, 3) and if this condition is met continue by using $P_j \leq [1-(1-0.1)^{1/k-j}$ where j = rank of variable, until the inequality is met or all P-values have been evaluated. Observed significance levels must be less than adjusted levels to achieve significance at the 0.1 level.

[d] P-values that were significant following Rice's sequential Bonferroni correction.

Table 14. Results of univariate comparisons of macro-habitat variables at ruffed grouse brood sites and random sites at Luther and Dean, Montana, 1997-1998.

Habitat Variable[a]	Brood Sites (n = 74) Mean	SE	Random Sites (n = 50) Mean	SE	Observed P[b]	Critical P[c]
DPOTR	8.61	3.84	55.57	10.47	<0.01[d]	0.03
DH2O	93.72	10.93	212.02	24.08	<0.01[d]	0.05
DC	25.88	5.14	38.77	8.54	0.17	0.10

[a] DPOTR = Distance to nearest aspen; DC = Distance to clearing (clearing is defined as an area with overhead canopy <15%); DH2O = Distance to any standing body of water.

[b] Observed significance level of T-test.

[c] Since 3 variables measured on the same plots were used to test for differences, Rice's sequential Bonferroni correction to assess significance of results was employed. This procedure involves: 1) ranking the set of P-values from smallest to largest, 2) determining if the smallest P-value is less than the Rice's adjusted P (i.e. $P_1 \leq [1-(1-0.1)^{1/k}]$ where k=number of variables, 3) and if this condition is met continue by using $P_j \leq [1-(1-0.1)^{1/k-j}$ where j = rank of variable, until the inequality is met or all P-values have been evaluated. Observed significance levels must be less than adjusted levels to achieve significance at the 0.1 level.

[d] Significant P-values following Rice's sequential Bonferroni correction.

Table 15. Multiple logistic regression models of micro-habitat and macro-habitat variables predicting the probability of ruffed grouse brood site selection at Luther and Dean, Montana, 1997-1998.

Model Type	logit[a]	Model evaluation[b] AIC	Δ AIC	R^2	P
Micro.[c]	-4.808 + 0.003(SHR) + 0.040(CC) + 0.031(GC) - 0.046(PICO)	127.70[f]	0.00	0.66	<0.01
	-5.487 + 0.003(SHR) + 0.039(CC) + 0.038(GC) + 0.020(POTR)	128.36	0.66	0.61	<0.01
	-5.651 + 0.003(SHR) + 0.042(CC) + 0.039(GC)	129.54	1.84	0.59	<0.01
Null[d]	0.392	169.23	41.53	<0.01	
Macro.[d]	1.608 - 0.025(DPOTR) - 0.005(DH2O)	135.13[g]	0.00	0.62	<0.01
	1.626 - 0.025(DPOTR) - 0.005(DH2O) - 0.001(DC)	137.08	1.95	0.62	<0.01
Null[d]	0.392	169.23	32.15	<0.01	

[a] Logit of the equation estimating the probability of brood site selection. Variables with positive coefficients are

Table 15. (continued)

positively related to a sites probability of being selected for brood-rearing.

[b] Model evaluation parameters are: Akaike's Information Criteria (AIC) which is used to select the most parsimonious model; Δ AIC which shows differences in AIC values among models; R^2 measures the proportion of the models log-likelihood explained by the model; P value is associated with a likelihood ratio test comparing the estimated model to the null model.

[c] Micro-habitat variable analysis.

[d] Null is a model with an intercept term only.

[e] Macro-habitat variable analysis.

[f] Most parsimonious model for micro-habitat variable analysis.

[g] Most parsimonious model for macro-habitat variable analysis.

The most parsimonious model produced by logistic regression for comparison of brood sites and random sites at the macro-site level included distance to aspen and distance to water (Table 15). This model was more parsimonious than the null model (Δ AIC 32.15) and had an R^2 value of 0.62. Logistic regression indicated that brood sites were closer to aspen stands and water than random sites. One other model was within 2 AIC units of the most parsimonious model and was included in the confidence list of models. This model included the same variables and coefficient signs as the most parsimonious as well as distance to clearing, which was negatively correlated to brood site selection.

Brood Habitat and Chick Survival

Univariate Analysis Univariate comparisons of micro-habitat at variables at sites used by broods experiencing >50% chick survival versus broods with lower survival indicated that broods with higher survival used sites with greater shrub-stem density ($\underline{P} < 0.01$)(Table 16). Univariate analysis of macro-habitat variables at sites used by broods experiencing >50% chick survival versus broods with lower survival indicated that broods with higher survival used sites that were further from water ($\underline{P} < 0.01$)(Table 17).

Multivariate Analysis The most parsimonious model produced by logistic regression for predicting chick survival by comparing micro-habitat variables included shrub stem density, sub-dominate conifer species stem density, and tree stem density (Table 18). This model was more parsimonious than the null model (Δ AIC 19.40) and had an R^2 value of 0.51. Logistic regression indicated

Table 16. Results of univariate comparison of micro-habitat characteristics at sites used by broods that experienced >50% chick survival and sites used by broods with lower survival at Luther and Dean, Montana, 1997-1998.

Habitat Variable[a]	>50% Chick Survival (n = 2) Mean	SE	<50% Chick Survival (n = 3) Mean	SE	Observed P[b]	Critical P[c]
CC	76.82	2.52	79.68	2.77	0.47	0.05
GC	51.30	3.88	43.54	2.45	0.08	0.01
SHR	691.64	40.84	467.70	37.55	<0.01[d]	0.01
SHRDV	7.67	0.38	7.87	0.26	0.62	0.10
SNG	11.43	1.73	17.05	2.15	0.06	0.01
TR	24.36	2.32	41.12	7.01	0.05	0.01
PSME	4.89	2.21	2.00	0.94	0.18	0.02
PICO	1.64	0.84	3.20	1.25	0.35	0.03
POTR	13.82	2.13	26.50	6.88	0.14	0.02
PIEN	2.00	0.75	6.57	1.58	0.02	0.01
POPSPP	0.00	0.00	0.07	0.05	0.26	0.03
CONSPP	0.89	0.45	0.12	0.09	0.04	0.01

[a] CC= % overhead canopy cover; GC= % ground cover composed of shrubs,

Table 16. (continued)

forbs, grass, and downed woody debris; SHR= # of shrub stems/plot >.4cm basal diameter; SHRDV= shrub diversity; SNG= # of snags > 2cm basal diameter and > .5m in height; TR= # of trees > 2cm basal diameter and > .5m in height; PSME=# of Douglas fir > 2cm basal diameter and > .5m in height; PICO= # of Lodgepole pine >2cm basal diameter and > .5m in height; POTR= # of Quaking aspen > 2cm basal diameter and > .5m in height; PIEN= # of Englemenn spruce > 2cm basal diameter and > .5m in height; POPSPP= # of trees of Cottonwood spp. > 2cm basal diameter and > .5m in height; CONSPP= # of trees of other conifer species (Abies lasiocarpa, Pinus flexilus, Pinus ponderosa, Pinus albicaulus) > 2cm basal diameter and > .5m in height. Species included in this variable were found on <10% of all sites.

[b] Observed significance level of T-test.

[c] Since 12 variables measured on the same plots were used to test for differences, Rice's sequential Bonferroni correction to assess significance of results was employed. This procedure involves: 1) ranking the set of P-values from smallest to largest, 2) determining if the smallest P-value is less than the Rice's adjusted P (i.e. $P_1 \leq [1-(1-0.1)^{1/k}]$ where k=number of variables, 3) and if this condition is met continue by using $P_j \leq [1-(1-0.1)^{1/k-j}$ where j = rank of variable, until the inequality is met or all P-values have been evaluated. Observed significance levels must be less than adjusted levels to achieve

[d] Significant P-values following Rice's sequential Bonferroni correction.

Table 17. Results of univariate comparison of macro-habitat characteristics at sites used by broods that experienced >50% chick survival and sites used by broods with lower survival at Luther and Dean, Montana, 1997-1998.

Habitat	>50% Chick Survival (n = 2)		<50% Chick Survival (n = 3)		Observed	Critical
Variable[a]	Mean	SE	Mean	SE	P[b]	P[c]
DPOTR	4.84	1.58	10.17	6.95	0.53	0.10
DH2O	154.28	18.85	50.67	10.18	<0.01[d]	0.03
DC	27.12	9.01	18.70	3.59	0.33	0.05

[a] DPOTR = Distance to nearest aspen; DH2O = Distance to any standing body of water; DC = Distance to clearing (clearing is defined as an area with overhead canopy <15%).

[b] Observed significance level of T-test.

[c] Since 3 variables measured on the same plots were used to test for differences, Rice's sequential Bonferroni correction to assess significance of results was employed. This procedure involves: 1) ranking the set of P-values from smallest to largest, 2) determining if the smallest P-value is less than the Rice's adjusted P (i.e. $P_1 \leq [1 - (1-0.1)^{1/k}]$ where k=number of variables, 3) and if this condition is met continue by using $P_j \leq [1-(1-0.1)^{1/k-j}$ where j = rank of variable, until the inequality is met or all P-values have been evaluated. Observed significance levels must be less than adjusted levels to achieve significance at the 0.1 level.

[d] Significant P-values following Rice's sequential Bonferroni correction.

Table 18. Multiple logistic regression models of micro-habitat variables predicting the probability of chick survival at Luther and Dean, Montana, 1997-1998.

Model Type	logit [a]	Model evaluation[b]			
		AIC	Δ AIC	R^2	P
Micro.[c]	-2.585 + 0.004(SHR) + 0.909(CON) - 0.021(TR)	73.07[e]	0.00	0.51	<0.01
	-3.092 + 0.004(SHR) + 0.807(CON) - 0.018(POTR)	73.75	0.68	0.47	<0.01
	-2.797 + 0.004(SHR) + 0.848(CON) - 0.041(SNG)	74.10	1.03	0.47	<0.01
	-2.730 + 0.004(SHR) + 0.764(CON) - 0.023(TR) + 0.036(PSME)	74.20	1.13	0.53	<0.01
	-3.387 + 0.004(SHR) + 0.911(CON)	74.43	1.36	0.53	<0.01
	-2.260 + 0.004(SHR) + 0.870(CON) - 0.019(TR) - 0.045(PIEN)	74.50	1.43	0.45	<0.01
	-2.483 + 0.004(SHR) + 0.870(CON) - 0.016(TR) - 0.018(SNG)	74.78	1.71	0.55	<0.01
	-2.643 + 0.004(SHR) + 0.764(CON) - 0.017(POTR) - 0.054(PIEN)	74.84	1.77	0.41	<0.01
	-2.385 + 0.004(SHR) + 0.976(CON) - 0.011(POTR) - 0.030(TR)	74.98	1.91	0.52	<0.01
Null[d]	0.479	92.47	19.40	<0.01	

Table 18. (continued)

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[a] Logit of the equation estimating the probability of chick survival based on habitat selection. Variables with positive coefficients are positively related to chick survival.

[b] Model evaluation parameters are: Akaike's Information Criteria (AIC) which is used to select the most parsimonious model; Δ AIC which shows the differences in AIC values among models; R^2 measures the proportion of the models log-likelihood explained by the model; P value is associated with a likelihood ratio test comparing the estimated model to the null model.

[c] Micro-habitat variable analysis.

[d] Null is a model with an intercept term only,.

[e] Most parsimonious model.

that broods experiencing greater survival rates used sites with greater shrub and sub-dominant conifer-species stem densities, and reduced tree stem densities. Eight other models were within 2 AIC units of the most parsimonious model and were included in the confidence list of models. All models in the confidence list included shrub stem density and sub-dominate conifer species stem density. Variables negatively correlated with survival included tree stem density, aspen stem density, snag and Englemann spruce stem density, which were included in 5, 3, 2, and 2 models respectively. Douglas fir stem densities were positively correlated with survival and was included in one model. The signs associated with coefficients for each variable were consistent across all models.

The most parsimonious model produced by logistic regression for predicting chick survival by comparing macro-habitat variables included distance to water (Table 19). This model was more parsimonious than the null model (Δ AIC 20.18) and had an R^2 value of 0.56. No other macro-habitat variables were entered into multiple logistic regression.

The most parsimonious model produced by logistic regression for predicting the effect of cover type and age on chick survival was the null model (Table 20). Nine other models were within 2 AIC units of the most parsimonious model and were included in the confidence list of models. All models in the confidence list except PM and PC were significantly better than the null model. However, none of the model's R^2 value exceeded 0.30, indicating that much variation in the data remains unexplained.

Table 19. Multiple logistic regression models of macro-habitat variables predicting the probability of chick survival at Luther and Dean, Montana, 1997-1998.

		Model Evaluation[b]			
Model Type	logit[a]	AIC	Δ AIC	R^2	P
Macro[c]	-1.732 + 0.015 (DH2O)	72.29[e]	0.00	0.56	<0.01
Null[d]	0.479	92.47	20.18	<0.01	

[a] Logit of the equation estimating the probability of chick survival based on habitat selection. Variables with positive coefficients are positively related to chick survival.

[b] Model evaluation parameters are: Akaike's Information Criteria (AIC) which is used to select the most parsimonious model; Δ AIC which shows the differences in AIC values among models; R^2 measures the proportion of the models log-likelihood explained by the model; P value is associated with a likelihood ratio test comparing the estimated model to the null model.

[c] Macro-habitat variable analysis.

[d] Null is a model with an intercept term only,.

[e] Most parsimonious model.

Table 20. Multiple logistic regression models predicting the effect of proportion of time spent in a specific cover type and age of chicks on chick survival at Luther and Dean, Montana, 1997-1998.

	Model Evaluation[b]			
Logits for candidate models[a]	$QAIC_c$	$\Delta QAIC_c$	R^2	P
1.756[c]	56.896	0.00	<0.01	
1.887 - 0.392(A1)[d]	57.086	0.19	0.18	0.02
1.943 + 0.496(Age)[e]	57.299	0.40	0.17	0.02
1.786 + 0.398(PA)[f]	57.646	0.75	0.14	0.05
2.140 - 0.082(A1) + 1.013(PA) - 0.664(A1PA)[g]	57.745	0.85	0.26	<0.01
1.916 - 0.403(A1) + 0.400(PA)	57.808	0.91	0.20	<0.01
1.964 - 0.613(A1) - 0.469(PM)[h]	57.843	0.95	0.21	<0.01
1.786 - 0.299(PC)[i]	58.060	1.16	0.11	0.10[j]
1.959 + 0.468(Age) + 0.358(PA)	58.319	1.42	0.19	0.02
1.753 - 0.111(PM)	58.826	1.93	0.04	0.56[j]

Table 20. (continued)

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[a] Logit of the equation estimating the probability of chick survival by age and cover type use. Variables with positive coefficients are positively related to chick survival.

[b] $QAIC_c$ is an AIC value that has been adjusted for small sample sizes and over dispersion. $QAIC_c$ =-2loglikelihood /c-hat + 2K (K + 1)/(n - ess - K - 1) where K= # of parameters, n-ess = effective sample size, and c-hat = overdispersion factor. Δ $QAIC_c$ shows the difference in $QAIC_c$ values among models. R^2 measures the proportion of the models log-likelihood explained by the model. P value is associated with a likelihood ratio test comparing the estimated model to the null model.

[c] Null model consisting of an intercept term only.,

[d] A1 represents a dummy variable coded such that 1=observations during a chicks first week post hatch and 0= observations during weeks 2 through 7 post hatch.

[e] Age represents the week in which observations on chicks were made.

[f] PA is the proportion of time broods were observed in aspen cover type.

[g] A1PA is an interaction term that is used when the effects of the predictor variables on the response variable are not additive but depend on the levels of other predictor variables. Thus, the effect of A1PA on chick survival depends on the levels of the individual variables A1 and PA.

[h] PM is the proportion of time broods were observed in mixed cover type.

[i] PC is the proportion of time broods were observed in coniferous cover type.

[j] Estimated model does not yield a better fit to the data than the null model.

DISCUSSION

Productivity

Nest Data

Productivity in my study area was lower than that typically reported for ruffed grouse. Although this may be typical of populations living in high-elevation sites of the Rocky Mountains, it is also likely that I was studying a marginal population as indicated by the low density of birds.

The nesting success rate of 0.42 reported for this study was lower than the mean rate of 0.61 reported from 13 studies summarized by Bergerud (1988a) from the midwestern and eastern United States and Canada. Additionally, the percentage of nests destroyed by predators (42%) in this study was greater than the percentage destroyed by predators in Bergerud's (1988a) summary. Although the diversity and density of the predator community in my study area is not fully understood, the predator composition could be responsible for the observed nest-predation rate. However, the percentage of nests lost to predation in my study is more comparable to that found in grouse populations at more southerly latitudes (Bergerud 1988a) where the abundance and diversity of predators is greater than that found in the Northern Rockies (McCoy and Conner 1980). This suggests that the predator community in my study area is an insufficient explanation for the observed nest-predation rate. I believe that the predation rate in my study was high due to the highly fragmented nature of the habitat on my study sites. My study sites consisted of coniferous forests dominated by lodgepole pine, with meadows and aspen stands interspersed throughout. Unlike areas in the eastern and midwestern United States where aspen stands may exceed 100 ha (see Yahner and Scott 1988) or be the dominant tree on the landscape (Mueggler 1985), aspen stands on my study site were <2 ha and constituted approximately 8% of the landscape.

Studies have indicated that forest fragmentation may increase nest predation in passerines by reducing patch size and overall habitat area, and by increasing the amount of edge: all factors that aid predators (Wilcove 1985, Andren et al. 1995). Similarly, Small et al. (1996) thought that most ruffed grouse nests that failed due to predation in their study were a result of extensive forest fragmentation. Although evidence suggests that forest fragmentation may be a sufficient explanation for the observed predation rates in my study, larger samples of nests and more information on the predator community are needed to verify this assumption.

In addition to predation and forest fragmentation, cover type has also been shown to affect nesting success (Bump et al. 1947, Maxson 1974). Studies from the midwestern and eastern United States suggest that hens will improve their probability of nesting successfully by choosing aspen over other cover types in which to nest (Bump et al. 1947, Maxson 1974). I did not detect a difference in nesting success between aspen and conifer cover types even though aspen cover was preferred. Failure to detect a difference could well be the result of low statistical power due to my small sample of nests (Steidl et al. 1997). Thus, it could be that differences exist. Results from my artificial nest study follow the pattern of other studies: nests in aspen were more likely to survive. Although results of artificial nest studies should be interpreted with caution (Major and Kendall 1996, Butler and Rotella 1998), the pattern should be investigated with adequate samples of real nests. This will be difficult, however, given current population levels.

Brood Data

Chick survival in this study (0.37) was similar to that reported from studies in the midwestern and eastern United States and Canada (Bump et al. 1947, Kupa 1966, Rusch and Keith 1971a). This is in keeping with Bergerud (1988a), who reported no significant differences in chick survival among forest, steppe, and tundra grouse. I was not able to determine causes of death for chicks, which is notoriously difficult because few chicks are recovered (Bump et al. 1947). Likely causes of mortality include weather, predation, physiological disturbance, and starvation (Bump et al. 1947, Larsen and Lahey 1958, Ritcey and Edwards 1963, Zwickel and Bendell 1967, Barret 1970). Given the poor information on causes of mortality, one must rely on information regarding habitat characteristics of sites with higher chick survival to infer causes of mortality and to make habitat management recommendations (see below).

Habitat Selection

Nest Data

The pattern and process of habitat selection are theorized to be a result of various selective forces (Morrison et al. 1992). By studying the pattern (differences in mean habitat variables between nest sites and random sites) and process (differences in mean habitat variables between successful and unsuccessful nests) of nest site selection, we can gain insight into the selective forces that are responsible for patterns of habitat use (Morrison et al. 1992) and what constitutes optimal habitat for nesting hens.

In this study, I achieved limited evidence of any pattern or process of nest-site selection. Nesting hens preferred aspen cover type with an elevated density of cottonwood stems. However, neither aspen cover type or stem density of cottonwood species were associated with higher nesting success. These results contradict Bump et al. (1947) and Maxson (1978) who reported increased nesting success in aspen/hardwood cover types. Also, all other mean habitat variables at successful nest sites were indistinguishable from unsuccessful nest sites, suggesting that no selection occurred (Clark and Shutler 1999). The lack of differences could be due to low statistical power associated with small sample sizes or because truly no differences exist.

Absence of selection may occur when predators use search images to locate nests, resulting in random nest placement being favored via natural selection (Martin 1988). It is quite possible that the small size and patchy distribution of aspen stands in this study provided predators with such a search image. In this type of scenario, predators are the main drivers of nest site selection and optimal habitat becomes difficult to define. Another possible interpretation of the lack of evidence of a pattern or process of nest site selection is that patterns reflect long-term optima for populations, even though they may be neutral or maladaptive in the short-term (Clark and Shutler 1999). Selection of nest sites containing aspen cover and cottonwood species during my study may represent selection that is based on a long-term strategy to avoid predation, but is seen as only neutral during the recent short-term period of habitat alteration due to fire suppression (Mueggler 1985). Since the turn of the century, forest management practices on my study area, most notably fire suppression, have resulted in approximately a 50% reduction in aspen (Pierson pers. comm.). My data do not provide answers, thus future research with adequate sample sizes should investigate these alternative hypotheses, as they have important implications for the ecology and management of ruffed grouse.

Brood Data

Contrary to findings for nest site selection, there was strong evidence indicating a pattern and process of site selection by broods in this study. Broods favored aspen cover and a dense understory. Because broods select sites based on their food and cover requirements (Bump et al. 1947, Bergerud 1988a), this pattern likely provides a long-term advantage to brood members.

Aspen stands in the western United States support a more diverse and dense understory than do adjacent coniferous stands (Mueggler 1985). Diverse understory may potentially help grouse chicks up to 2 weeks of age meet their food requirements by increasing insect diversity (Strong et al. 1984). Also, older chicks, who are predominately vegetarian and consume a wide variety of plants (Bump et al. 1947), may also benefit from increased understory diversity. Dense understory may provide shelter from severe weather events (Bump et al. 1947) and escape cover from predators (Gullion 1962, Nichols and Warner 1972). This suggests that aspen cover type and its associated understory are selected for because they can more adequately meet the food, shelter, and escape cover requirements of chicks than do conifer cover types.

Although the pattern of brood site selection in this study appears to incorporate both the food and cover requirements of chicks, it does not provide insight into which or either of these requirements is the ultimate factor in site selection. However, by examining the process of brood site selection (differences in characteristics of chicks experiencing different survival rates), it becomes apparent that cover requirements may be more influential in brood site selection.

Bergerud (1988b) speculated that dense understories failed to produce a sufficient diet of insects, resulting in lower survival rates for blue grouse chicks inhabiting these areas. Because the amount of light in a system exerts a major influence on the ability of almost all insects to survive and multiply (Gillott 1980), dense understories may limit the abundance of insects by reducing the amount of light penetration to the forest floor. I, however, found that survival rates increased with shrub density. This suggests that even in dense understories, insect availability was not a limiting factor for young chicks in this study. Additionally, the wide variety of plant material reportedly consumed by older chicks (Bump et al. 1947, Korschgen 1966) and their ability to adjust their diets in accordance with food availability (Korschgen 1966) indicates that food is also not limiting for older chicks. Therefore, the higher survival rates for chicks in broods that used relatively denser shrub cover was more likely a response to improved escape cover from predators than an increase in forage opportunities.

The fact that broods with > 50% chick survival were typically found further from water than broods with lower survival rates, may also indicate the role of predation in brood-site selection. Riparian habitats in the western United States are linear, patchy, and rarely > 150 m from habitat edge (Tewksbury et al. 1998). Fragmented habitats such as these have been reported to contain abundant complexes of predators (Keith 1983) and be areas of concentrated activity for some mammals (Bider 1968). Therefore, broods that concentrated their activities in upland sites may have reduced their contact with predators and improved their chick survival.

Conclusions

Data from this study suggest that predation may be the factor most limiting productivity and the main force behind habitat selection. Data from this study indicate that hens using aspen cover type versus conifer cover types experience greater productivity.

The low nesting success in this study was directly related to a high incidence of nest predation. Although nesting success did not differ between cover types, the fact that aspen was preferred for nesting indicates that this cover type historically conveyed some advantage to hens. The reduction of aspen on the landscape since the turn of the century is likely responsible for aspen being seen as only neutral habitat for nesting hens during the short duration of this study. Under these circumstances it is difficult to define optimal nesting habitat.

Broods that spent a greater proportion of their time in aspen, and used sites with denser understories, experienced higher chick survival rates. Because food is likely not limited for chicks, higher survival rates for broods using dense understories was likely due to improved escape cover from predators on dense sites. Therefore, it appears that aspen and their associated understories, which are denser and more diverse in the western United States than their adjacent coniferous counterparts (Mueggler 1985), are better at providing the cover requirements for chicks. Although, aspen was seen as only neutral habitat in terms of nesting success, the increase in chick survival for broods using aspen indicates that net productivity will be greater for hens that use aspen.

Although nesting success and habitat used for nesting in this study did not entirely agree with studies from the midwestern and eastern United States and Canada, chick survival and habitat used during the brood period were quite similar. This suggests that management strategies designed and implemented in other parts of the United States and Canada to enhance ruffed grouse productivity may be applicable to areas in the Northern Rockies consisting of aspen/conifer mosaics dominated by lodgepole pine. However, management strategies recommend creating stands of different age classes of aspen to accommodate the changing needs of ruffed grouse during their life-cycle (Gullion 1984). In areas where aspen stands are small and patchy and part of an aspen/conifer mosaic, large movements through coniferous stands would be required to use these different age class aspen stands. However, this study indicated that chick survival was negatively effected by the proportion of time chicks spent in conifer. Thus, populations of ruffed grouse in the Northern Rockies will likely never reach the densities observed in other parts of the country. Population parameters and habitat estimates in this study were calculated from small samples. Thus, continued research to substantiate these estimates is recommended.

SCOPE AND LIMITATIONS

The research conducted in this study was descriptive in nature. Although descriptive studies are an essential phase of wildlife studies, they involve wide objectives rather than tests of specific hypotheses (Ratti and Garton 1994). Thus, the certainty of conclusions in this study and the inference space to which they are applicable is limited (Ratti and Garton 1994). Despite limitations, descriptive studies such as mine are important to wildlife managers interested in species or populations of species about which little is known because they provide the information that can form future research hypotheses (Ratti and Garton 1994).

Related to the descriptive nature of this study was the *post-hoc* model selection process addressing various aspects of nesting and brood-rearing ecology. Because very little is known about ruffed grouse ecology in the Northern Rockies no *a priori* models were constructed and all data analysis was *post hoc.* Model construction via *post hoc* analysis probably overfit the data and over-estimate precision (Burnham and Anderson 1998). Thus, the actual predictive performance of the models generated in this study may be below what might be expected from the statistics associated with the final analyses (Burham and Anderson 1998).

Additionally, as in other studies addressing ruffed grouse productivity, this study suffered from small sample sizes. Small sample sizes reduce the precision of an estimator or a statistic and reduce the power of tests (Ratti and Garton 1994). Reduced precision is reflected by wider confidence intervals and larger standard errors associated with estimates (Ratti and Garton 1994). Thus the wide confidence intervals and large standard errors associated with nest site selection by cover type, nesting success, habitat variables at successful and unsuccessful nests, and chick survival indicate that these estimates lack precision and should be interpreted with caution.

RESEARCH RECOMMENDATIONS AND MANAGEMENT IMPLICATIONS

I developed the following research recommendations and management guidelines for maintaining or increasing ruffed grouse populations in habitats consisting of aspen/conifer mosaics dominated by lodgepole pine in the Northern Rockies.

1) Results from my study are similar in numerous ways to results from studies in the midwestern and eastern United States. Thus, management strategies for these areas may be beneficial in the Northern Rockies. However, if managers implement management plans based on results of my study, I strongly urge that it be done in conjunction with continued research of nesting and brood-rearing hens to achieve confirmatory results with greater sample sizes. I recommend emphasizing study of nesting success, the main driver of productivity (Beregerud 1988a), and nesting habitat and its relationship to productivity. Future projects should intensify trapping effort to increase the sample size of nesting hens.

2) Management should seek to maintain or improve productivity by preserving and/or regenerating aspen stands in their region. In my study, aspen cover was preferred by nesting and brood-rearing hens. Further, broods that spent a greater proportion of time in aspen experienced higher chick survival rates. Thus, productivity was greater in aspen than in conifer. Data from this study suggest that regeneration of aspen designed for brood-rearing habitat should emphasize upland sites within close proximity to water (approximately 150m), but not directly adjacent to water.

3) Aspen regeneration projects target mature to over-mature stands and require clear cutting of selected stands. However, stands in these age classes reportedly provide optimal winter food and cover requirements (Gullion 1984). Thus, future research should investigate the habitat needs of wintering birds to evaluate the impact of regeneration projects on this stage of the life-cycle.

4) The stem density of cottonwood species was greater at nest sites than at random sites. Although the role of cottonwood species at nest sites was unclear, cottonwood species should be preserved during any aspen regeneration projects until this relationship is better understood.

5) Although the relationship between productivity and cover type was addressed in this study, landscape scale characteristics of habitats used, such as patch size and surrounding landscape configurations were not. These factors are crucial in determining which aspen stands should be regenerated because patch size has been shown to have an effect on nest predation (Wilcove 1985) and the abundance of predators in a local area may be influenced by the surrounding landscape (Donovan et al. 1997). Thus, future research of habitat use should be expanded to include more landscape scale characteristics.

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APPENDICES

Appendix A. Artificial nest success results in aspen and conifer cover types using predation criteria 2[a] in Luther and Dean, Montana, 1998.

Habitat type	Nests (n)	Mean	SE
Aspen[b]	41	0.53[c]	0.08
Conifer[d]	21	0.14	0.08
Total[e]	62	0.40	0.06

[a] Proportion of nests in which either egg was moved, missing, crushed, or the clay egg had visible signs of predation from any predator.
[b] X^2 indicated no significant difference ($\underline{P} = 0.90$) between artificial nest success in aspen and natural nest success in aspen.
[d] X^2 indicated no significant difference ($\underline{P} = 0.49$) between artificial nest success in conifer and natural nest success in conifer.
[e] X^2 indicated no significant difference ($\underline{P} = 0.81$) between overall artificial nest success and overall natural nest success.

Appendix B. How to convert micro-site area and micro-site habitat variables from Metric to English measurements.

1) Micro-site areas equals approximately 1/18 of an acre.
2) Micro-site habitat variables can be converted into per acre amounts by multiplying by 18.