# Relationships Among Behavior, Habitat, and Population Density in a Cyclic

# Population of Ruffed Grouse

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O'Connell, Marie Hemmen, Jennifer Larson, Ben Reinhardt and family, Bryan Fisher, Sheryll and Steve Garbe and several others for guidance and friendship.

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## DEDICATION

To all of the teachers and mentors who had faith in me and helped me along the way.

**ABSTRACT**

Understanding how patterns of habitat use by animals vary in relation to

population density is of major interest to ecologists and wildlife managers.  For decades,

biologists have linked high populations of ruffed grouse (*Bonasa umbellus*) with aspen

(*Populus* spp.) forests in the northern part of their range.  However, male ruffed grouse in

northern populations also select territories in conifer forests, even when apparently

suitable aspen forests nearby remain vacant.  This selection of cover types that are

presumed to be of lower quality presents a conundrum to biologists: why would males

select inferior cover types when better cover types are available?

To address this conundrum, I investigated the behavior, habitat, and population

dynamics of a population of male ruffed grouse to evaluate relationships among these

factors and elucidate mechanisms of their cover type selections.  Little is known about

the mechanisms underlying habitat selection in most species.  Studying the behavior of

individuals within a population is one technique used to evaluate these mechanisms.

Ruffed grouse are an ideal species in which to study behavior, habitat, and population

dynamics because the males are easily counted, they are territorial, their territories are

relatively easy to locate, and many populations are cyclic.  I conducted my study at the

Cloquet Forestry Center in northern Minnesota and used data collected over the course of

one complete 10-year ruffed grouse population cycle (2002-2011) during which time the

population reached both a high and low point in the numbers of territorial males counted

each year.  The grouse population was declining when the study begin in 2002 and did

not begin its cyclic increase until 2006.  I used repeated auditory surveys to locate the

territories of drumming males and estimate the population density of territorial male

grouse. I assessed behavior questions by using automated video systems to record the activities of a stratified (by aspen and conifer cover types) random sample of 23 male ruffed grouse from all of the males detected on my surveys. The number of breeding males on my 1,419-ha study area varied from a low of 47 in 2005 to a high of 134 in 2010. I assumed that rates of male ruffed grouse display were indicative of their interactions with conspecifics. I developed *a priori* models that described the relationships among male display rates and environmental attributes, structured these models as generalized linear models, and used information theoretic model selection to evaluate these models. The null model (i.e., intercept only model) was the top-ranked model (received the lowest $AIC_c$ score).

I used generalized linear models with random effects and information theoretic model selection to evaluate *a priori* models that described relationships among male ruffed grouse densities per cover type and environmental variables associated with their territory locations. Aspen-dominated cover types contained the highest densities of male ruffed grouse during all years (0.09 to 0.24 males/ha during 2002-11) except 2006 and 2011, when density was highest in northern hardwoods-dominated cover types (0.12 and 0.13 males/ha in 2006 and 2011, respectively) followed by aspen-dominated cover types (0.10 and 0.12 males/ha in 2006 and 2011, respectively). The density of males in conifer-dominated cover types was always less than the density of males in aspen-dominated cover types (0.02 – 0.08 males/ha during 2002-11). In addition to consistently higher densities of males in aspen- versus conifer-dominated cover types, densities of males in aspen-dominated cover types exhibited a higher intrinsic rate of increase than in conifer-dominated cover types during all years. However, the consistent occupancy of

conifer-dominated cover types by males throughout the study also suggested that males perceived conifer-dominated cover types as suitable sites for territories and display behavior.  At the cover type scale, the top-ranked model related to male grouse population density included an interaction of cover type and year variables.  The mean density of male ruffed grouse within landscapes during all years ranged from 0.04 to 0.10 males/ha with minimum and maximum densities of 0 and 0.16 males/ha, respectively, during the entire study.  At this landscape scale, an interaction of the estimate of the relative evenness of cover types (Shannon's Evenness Index) within landscapes and year comprised the top-ranked model explaining male ruffed grouse densities.

Based on my study, if there is a difference in quality of conifer and aspen cover types, it manifests itself either in the specific stand structure used for male breeding displays or some life stage or seasonal habitat need of the ruffed grouse other than male breeding display cover.  My results show that grouse populations achieve their highest densities in heterogeneous landscapes when aspen-dominated cover types, composed of multiple age classes, are the key cover types on landscapes.  Landscapes that are less heterogeneous and where the majority of cover types are not dominated by aspen also harbor grouse, but at lower densities than heterogeneous aspen-dominated landscapes. Traditionally, managers have focused on the distribution and abundance of aspen-dominated cover types to enhance ruffed grouse habitat.  However, my findings suggest that managers should focus on managing the spatial complexity of cover types on landscapes, even when aspen-dominated stands are in low abundance.

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## INTRODUCTION

Habitat selection is a behavioral process, yet behavioral data are rarely used to test predictions about observed or inferred patterns of habitat selection because behavior is difficult to observe (Nocera and Forbes 2010). Habitat selection decisions affect an individual's fitness through survival or reproduction (Fretwell and Lucas 1970). Thus, examining wildlife behavior improves our knowledge of a species' habitat needs (Sutherland 1996, Ahlering and Faaborg 2006). Although the ruffed grouse (*Bonasa umbellus*; hereafter grouse) is one of the most intensively managed species in North America, very little is known about either the mechanisms or behavior underlying their habitat selection (Rusch et al. 2000).

Grouse are found in many cover types, but are strongly associated with aspen (*Populus* spp.) over most of their range because it provides all of their requirements throughout their life cycle. In addition, grouse population densities are highest in aspen-dominated landscapes (Gullion and Marshall 1968, Svoboda and Gullion 1972, Rusch et al. 2000). Consequently, aspen is presumed to be their optimal cover type. Males defend a territory centered approximately around their primary and alternate display sites (Rusch et al. 2000). These territories are often referred to as activity centers in the literature

(Gullion 1967). Males establish these territories primarily in young (10- to 25-years old), dense, aspen-dominated forest stands (hereafter aspen) for breeding display sites (Gullion and Marshall 1968).

The close association of grouse with aspen in the northern part of their range is primarily a function of protection from predators (particularly raptors; Gullion and Marshall 1968, Dessecker and McAuley 2001) and availability of food. Aspen catkins are the most nutrient-rich food available during the winter (Jakubas and Gullion 1991). In addition, grouse in northern MN survive best in forests that are not dominated by conifers (Gullion and Marshall 1968). The conifers of particular concern are "high-tree" pines (i.e., pines that have no branches near the ground) because such trees provide hunting perches for raptors (Dessecker and McAuley 2001). These observations contrast with those from previous studies in the eastern United States where conifers were a presumed habitat requirement (Bump et al. 1947). Additionally, in warmer parts of the grouse range, cover types other than aspen produce food year-round. Thus grouse in these areas use several cover types in addition to aspen (Atwater and Schnell 1989). These contrasting observations from northern MN versus these other locations in the grouse range precipitated a "conifer controversy" about the relative value of aspen and conifer as grouse habitat (Gullion 1990a). Gullion's career in grouse research culminated in an apparent concession that coniferous forest may be an acceptable cover type for ruffed grouse in MN if "islands" of aspen of at least 0.4 ha in size were allowed to develop within these conifer forests (Gullion 1990b). His caveat was that there must be some mature aspen (i.e., food source) within 200 m of territories or the territories would

not be occupied.

In many areas where aspen occurs some males select territories in conifer-dominated forest stands (hereafter conifer), which is presumed to be a suboptimal cover type, even when nearby and presumably suitable aspen is vacant and competition for these sites is low (i.e., low points in the population cycle; Zimmerman et al. 2009). However, Zimmerman et al. (2009) showed that populations of male grouse occupying aspen in northern MN experienced a higher intrinsic rate of population growth than those occupying conifer, and that their selection of conifer stands was "constrained" by the availability of aspen inclusions or dense understory structure within these conifer stands (Zimmerman and Gutiérrez 2008). Theory predicts that grouse selecting territories in conifer should have lower fitness relative to those selecting territories in aspen (Fretwell and Lucas 1970). Hence, selection of presumed suboptimal cover types presents a conundrum to biologists interested in understanding their habitat selection: are male ruffed grouse simply making mistakes (e.g., have imperfect knowledge; Fretwell and Lucas 1970) or are there other reasons why they select these cover types (e.g., male grouse are successful attracting mates in these cover types)? The "conifer controversy" regarding forest management for grouse (Gullion 1990b) has not been fully resolved. I attempted to address this long-standing controversy from a behavioral perspective. If conifer was a suboptimal breeding cover type relative to aspen, as has been suggested repeatedly in studies conducted in the upper Midwest (Gullion and Marshall 1968, Svoboda and Gullion 1972, Rusch et al. 2000), then I predicted that male grouse would behave differently when occupying suboptimal versus optimal cover types by having

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different rates of visual or drumming displays.  I evaluated this prediction by integrating

observations of territorial male grouse behavior with the cover type selected.  I predicted

that male grouse selecting conifer would have fewer interactions with conspecifics and

would need to display (i.e., drum) more frequently to attract mates than those males

selecting aspen because aspen is presumed to be the higher quality cover type.  Because I

expected conifer males to have fewer encounters with other grouse, I also expected them

to exhibit a lower rate of visual display because these displays are only performed when a

conspecific is in close proximity.  Finally, I predicted that territories of males inhabiting

conifer would be closer to the territories of males inhabiting aspen than the territories of

other males inhabiting conifer.  I predicted this scenario would occur because males

inhabiting conifer would try to increase their chance of (1) intercepting and mating with

females that were visiting aspen males, or (2) taking over a territory in aspen if one is

vacated.

## METHODS

### STUDY AREA

My study area was the 1,419-ha Cloquet Forestry Center (CFC; 46˚ 31' N, 92˚ 30'

W) in northern Minnesota (MN), USA, located in Carlton County, MN.  CFC was 60%

conifer (245 stands of red pine [*Pinus resinosa*], jack pine [*Pinus banksiana*], white

spruce / balsam fir [*Picea glauca* and *Abies balsamea*, respectively], black spruce [*Picea

mariana*], tamarack [*Larix laricina*], and northern white cedar [*Thuja occidentalis*]; range

and mean of stand sizes = 0.13 - 61.20 ha, 2.63 ha) and 19% aspen (96 stands; range and

mean of stand sizes = 0.13 - 12.30 ha, 2.56 ha; Loeffelholz and Zimmerman 2005).

Forest stands were defined as contiguous populations of trees that were considered

individual units and classified by the tree species composing >66% of the stand (Smith et

al. 1997).  My study area was ideal for this type of study because it was an experimental

forest, with many cover types present that were in various stages of succession.   Thus

CFC was a heterogeneous environment that allowed all grouse multiple choices of types

and ages of cover in which to display.


**LOCATING GROUSE TERRITORIES**

During the breeding seasons (first week of April to second week of June) of 2007-

2009, I conducted auditory surveys of displaying male grouse along permanent survey

transects that covered the entire study area (Zimmerman 2006).  My surveys were based

on a robust design (Cormack 1964, Jolly 1965, Seber 1965, Pollock et al. 1990) that

included repeated surveys distributed over three sampling periods: beginning, middle,

and end of the breeding season.  I made these sampling period distinctions because

grouse exhibit temporal variation in drumming (Gullion 1966) and because the

probability of detecting a male grouse increases with multiple surveys (Zimmerman and

Gutiérrez 2007).  I conducted 5 surveys (one each day) in each of 3 weekly open

sampling periods for a total of 15 surveys per transect during each breeding season.  Each

sampling period was separated by a two-week non-sampling (open) period.  During each

sampling period, I assumed the population to be closed to emigration, immigration, birth

(in our case, hatching did not occur until after the sampling season had ended), and death.

During each non-sampling period, I assumed the population to be open to emigration, immigration, birth (see above), and death. I randomly selected the order in which transects were surveyed during each sampling period. I also randomly assigned all observers to surveys with the criterion that each observer had to survey each transect at least once during each sampling period. Surveys began 30 min before sunrise and continued throughout the early morning (daily peak activity time of grouse; Rusch et al. 2000). The duration of surveys depended on the number of males detected along the route and the number of drumming structures that were located, but increased effort on transects that had a higher density of grouse did not affect counts (Kouffeld et al. 2013). Once a bird was heard drumming, the observer estimated its position by compass triangulation and then stealthily approached the bird to visually confirm its true location. The exact location of the bird was then recorded using a global positioning system unit. Visual confirmation also allowed observers to determine if this was the only bird drumming in the local area (i.e., sometimes birds were located near each other or in a direct line from the initial observer position so that auditory detection alone could result in an under-estimate of the number of birds in the same general area). Observers did not survey during conditions that impeded their ability to detect the birds (e.g., heavy rain/snow or wind). I used both a geographic information system (GIS)-based map of cover types (Loeffelholz and Zimmerman 2005) and direct observation to confirm the stand types occupied by individuals.

**SELECTION OF GROUSE FOR BEHAVIORAL OBSERVATIONS**

I located all actively drumming males that I could detect on the study area regardless of the cover type that they inhabited. Males established territories in aspen, conifer, birch, northern hardwoods, mixed hardwood conifer, bottomland hardwoods, forested wetlands, lowland brush, or upland brush. However, the primary cover type where males established territories was aspen, followed by conifer (see *RESULTS)*. Thus I used video to record observations of male grouse only in aspen or conifer. Because many fewer males selected territories in mixed hardwood-conifer forest stands and to be able to distinguish between effects of aspen versus conifer on male behavior, I avoided observing males in the mixed hardwood-conifer stand type. Prior to the beginning of each breeding season I randomly selected sites in both aspen and conifer forest-stands that had been used by males the previous year. I then confirmed during initial surveys that these sites were currently occupied by males. If males were not occupying selected sites in the current year, I randomly selected another site and determined presence as above. Sites were selected without replacement among years to avoid selecting the same individual in multiple years (a male will frequently use a site perennially). Though it is not likely that I selected the same male multiple times, given that not all of the males in this population are marked, I cannot rule out the possibility that one individual used multiple territories and was sampled more than once during the study (i.e., if the individual left his territory and took over a different territory in a later year). However, we think this has a relatively low probability (Zimmerman et al. In Review).

The number of males selected was dependent upon the number of recording

systems I had either available each year or that remained operable throughout the breeding season (e.g., black bears, *Ursus americanus*, would occasionally destroy a system). I used two types of automated video-recording systems (see below) to record male grouse at their display sites. I later reviewed these videos to quantify male behaviors. Males displayed from the same (primary) elevated structure (e.g., log, stump, dirt mound, boulder) in their territory throughout the breeding season (Gullion 1967). Their fidelity to these structures allowed for accurate placement of cameras to record the majority of their display activities. Their display habitat was characterized by a very high density of small diameter trees or shrubs, which required placement of video cameras close (6-8 m) to the display site to view the bird. This close placement restricted the camera's field of view so that individuals visiting males were not always observed.

In 2007, I used analog video-recording systems (SuperCircuits, Inc., Austin, Texas) consisting of cameras that recorded black and white footage and also were capable of recording infrared footage (to record grouse activity during dark hours in addition to daylight hours). These cameras were connected to videocassette recorders (VCRs; these recorded a frame rate of five frames per second, slow enough for video tapes to record continuously for 24 hrs but fast enough to be considered "continuous" recording) that recorded onto video home system (VHS) tapes. The video systems were powered by 12 V, 125 Ah marine deep-cycle batteries which, along with VHS tapes, I changed daily. VCRs were housed in durable, waterproof Pelican cases (CPD Industries, Montclaire, California). In 2008-09 I continued to use these analog systems, but also started using digital systems, which consisted of the same black and white infrared

cameras connected to digital video recorders (DVR; Fuhrman Diversified, Inc., Seabrook, Texas), and powered by two 12 V, 10 Ah lithium ion batteries.  I recorded video footage onto 8 GB secure digital high capacity (SDHC) flash memory cards; batteries and memory cards recorded continuously for 48 hrs before needing to be changed due to low remaining storage space or power.  DVRs were housed in durable, waterproof cases (DVR cases were custom made by Fuhrman Diversified, Inc.).  All video systems recorded continuously (24 hrs/day, 7 days/week) for the duration of the 9-week breeding/survey season.  Because of the large number of videos that I obtained, I randomly selected the days from which to review video from all of the days for which I had footage, and limited my review to the peak activity period (0400 to 1000h) of males (Rusch et al. 2000).  Thus I observed only a subset of male activity, but I predicted that if there were differences in male display behavior between cover types, these differences would be more readily detected during their peak activity period because that is when most females are visiting drumming logs.  Additionally, I did not constrain my selection of videos by the time of breeding season.

### DATA ANALYSES

I used information-theoretic model-selection to rank a set of *a priori* models using Akaike's Information Criterion adjusted for small sample sizes (AICc; Burnham and Anderson 2002).  Models were considered competitive if their AIC rankings were <2 AIC units apart (Burnham and Anderson 2002).  The response variables for all models were rates of visual or auditory displays.  I generated all models as negative binomial

generalized linear models with a log link.  I conducted all analyses using package *MASS*

version 7.3-16 (Venables and Ripley 2002) in program R version 2.14.1 (R Development

Core Team 2011).

### *A PRIORI* MODELS AND RESPONSE VARIABLES

The ruffed grouse is a promiscuous species (Wiley 1974).  Females of other

species that exhibit a promiscuous breeding system often have large home ranges that

may overlap the territories of several males (Wiley 1974).  When this occurs, males have

a relatively difficult time finding mates, which subsequently affects male spacing and the

strategy that males use to compete for females (Höglund and Alatalo 1995).  Hence, the

number of females that visit a male could reflect either the quality of the male or the

quality of the habitat.

I used the rates of drumming (i.e., drumming display rates; see below) and visual

displays (see below) as response variables to ascertain the effect of cover type on the

effort males expended to advertise (to attract females and deter males), and the amount of

interaction that males had with conspecifics, respectively.  I initially intended to use male

encounter rates with females as a response variable instead of visual display rates.

However, the limited area that was in view of cameras often precluded identification of

the sex of birds visiting males.  That is, for the majority of encounters, males displayed to

another grouse and then left their display structures presumably to interact with the

conspecific off-screen.  The initial physical display of males upon seeing either a female

or a rival male (hereafter visual display) is similar; thus it was impossible to always

distinguish the likely sex of the bird to which a male was displaying (Rusch et al. 2000). Consequently, I was constrained to measure rates of interaction with other grouse (male or female) by recording visual display rates rather than female visitation rates as a response variable. I quantified the number of both visual and drumming displays as rates (displays per hour) to account for variation in my viewing effort (the number of hours of video footage I reviewed for each male). In using display rates as a measure of interaction with other grouse, I assumed that males exhibited visual displays only to other grouse and not to other wildlife species. I did not evaluate the validity of this assumption in this study, though it is possible that males displayed to other species. In addition, males were not on their logs constantly; there were times when the male would disappear from view. Therefore it is possible that displays occurred off-screen that I could not observe.

A drumming display is an auditory display that functions to attract potential mates as well as announce territories to other males (Gullion 1967). For this display, the sender and receiver do not have to be in close proximity. The display is often initiated by the sender without solicitation from, or in response to, another individual. This display consists of males perching on elevated structures (hereafter drumming structures), using their tails to brace themselves, and beating their wings back and forth 40-55 times in rapid succession over 8-11 sec (Garcia et al. 2012). This wing movement creates a momentary vacuum by a sudden compression and release of air, which produces a sound similar to a miniature sonic boom (Rusch et al. 2000).

Males perform a "visual display" when they visually detect a conspecific. This

display consists of males fanning their tail, erecting their neck ruff (modified neck

feathers), and often strutting along their drumming structure before leaving it either to

deter a male competitor or to solicit mating with a female (Allen 1934). I consider this

display as a measure of conspecific encounter rates (male or female). I predicted that

male grouse in conifer would receive fewer conspecific visits and would consequently

expend more energy to attract females (i.e., drum at a higher rate) but perform fewer

visual displays. Thus I predicted that the drumming and visual display rate response

variables were not correlated.


**Model Development**

I developed five *a priori* models (Table 1.1) and analyzed these models twice for

two different response variables: visual display rate and drumming display rate. I

included an intercept only model (i.e., the null model) for each response variable to

evaluate the explanatory power of the variables I chose (Table 1.1, model 1). I

considered year-only models (Table 1.1, model 2) and included year in all other models

as a fixed, categorical variable (Table 1.1, models 3 - 5) to account for variation due to

the population size each year (Fig. 1.1). I predicted that the increase in the density of

grouse each year would affect individual behavioral dynamics by changing access to

mates and increasing competition. I expected that there would be an interactive effect of

several variables with year such that the effects of these variables would be smaller and

become diluted as the density of males increased each year. I expected this result

because the optimal (aspen) cover type would become saturated due to a higher number

of individuals in the population, causing individuals to use a wider variety of cover types than would be used in a lower-density year, when individuals could be more selective.

**Cover type**

I predicted that males occupying aspen would have different drumming and visual display rates than males occupying conifer because these cover types are presumed to differ in quality (Gullion and Marshall 1968). Aspen is considered preferable because it provides dietary needs (Jakubas and Gullion 1991) and optimal protective cover (Dessecker and McAuley 2001). Thus, I evaluated a cover type ("cover") model and included a cover type by year interaction (Table 1.1, model 3) because I predicted that the influence of cover type would differ depending upon population density (i.e., vary by stage in the population cycle). For the drumming display rate response, I predicted that drumming rates would be greater in conifer than aspen because conifer has been presumed to be suboptimal and males using conifer stands would have to advertise more frequently to attract mates. For the visual display rate response, I predicted that males in conifer would have lower rates because there would be fewer opportunities to interact with conspecifics (lower density in suboptimal conifer stands; Zimmerman et al. 2009).

**Nearest Neighbor Distance (NND)**

Although male grouse maintain territories, males sometimes settle so close to each other that they appear clustered in space (Gullion 1967;1976). Males of some other grouse species cluster together (i.e., form leks) when they display during the breeding

season because clustering provides a strong collective signal, which attracts more females than would a single male (Otte 1974, Bradbury 1981, Queller 1987, Alatalo et al. 1992). In the case of ruffed grouse, males may be choosing territories close to other males based on the quality of their neighbor's cover type, their neighbor's status, or because they are inexperienced and may be relying on conspecific cues to assess cover type quality (Seamans and Gutiérrez 2006, Ahlering et al. 2010, Nocera and Forbes 2010). In addition, males may choose to settle near more dominant males because they are likely to encounter more females and thereby increase their reproductive success (Foster 1983, Alatalo et al. 1992, Ahlering and Faaborg 2006, Campomizzi et al. 2008), or to secure a better site if the owner dies or leaves (Beletsky and Orians 1989).

Thus I included the NND variable in *a priori* models (Table 1.1, model 4). I calculated NNDs in ArcGIS v 9.3.1 (ESRI Inc., Redlands, CA) using Geospatial Modelling Environment 0.3.2 Beta (Beyer 2012), which required StatConnDCOM 3.1-2B6 and R v 2.11. The range of NND values was 70.77 – 610.59 m with a median of 158.01 m. I analyzed a year by NND interaction in this model because I predicted that year (mainly through changes in population size during the cycle) would affect NND and its influence on the response variables. Similarly, I included a model with year, cover, NND, and their interactions because I predicted that these variables acted in concert to influence the response variables (Table 1.1, model 5), with the NND effect changing each year as the population size increased. I also expected that both visual and drumming display rates for all males changed as a function of NND. I predicted multiple options for the impact that year would have on NND, and then the resulting NND effect on display

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rates.  First I predicted that NND may decrease as the population size increased because there were more individuals around in general and densities in all cover types would increase (no individuals would be completely excluded from occupying territories).  If this relationship was true, I predicted that male neighbors with smaller NNDs that were in closer proximity to each other would display more as a deterrent to conspecifics or to compete for mates.  Second, I predicted that competition for the best territories might intensify as the population increased because the opportunity for mating would increase with more females in the population.  This competition would be reflected in the NND such that NND would increase between male neighbors.  If this relationship occurred, I predicted two possible outcomes on male display rates: (1) males would display less frequently because they were farther apart and did not need to deter conspecifics as often, or (2) males would display more frequently because they had to work harder to attract females (this assumes that a lower density of males in a location attracts fewer females due to less stimulus).

**RESULTS**

<span style="font-variant: small-caps;">Surveys</span>

During 2007-2009, I located 63, 66, and 111 territorial male grouse, respectively (Fig. 1.1).  The majority of territories were in aspen sites each year, (2007: 57%; 2008: 52%; 2009: 58%), with conifer used secondarily (2007: 27%; 2008: 29%; 2009: 29%). The remaining males established territories in other cover types including birch, northern hardwoods, mixed hardwood conifer, bottomland hardwoods, forested wetlands, lowland

brush, or upland brush. The percentage of display sites that were utilized once versus used in two or three study years from 2007-2009 was similar between aspen and conifer. Of all aspen sites used by male grouse during the study, 68% were used 1 year, 21% were used 2 years, and 11% were used 3 years. Of all conifer sites used by male grouse, 68% were used 1 year, 20% were used 2 years and 11% were used 3 years.

DRUMMING AND VISUAL DISPLAY RATE MODELS

I quantified drumming and visual display rates for 12 males using aspen and 11 males using conifer sites (2007: 3 aspen, 3 conifer; 2008: 4 aspen, 5 conifer; 2009: 5 aspen, 3 conifer). For all aspen males, I reviewed 775, 883, and 652 hrs of video footage from 2007-2009, respectively. For all conifer males, I reviewed 280, 836, and 384 hrs of video footage from 2007-2009, respectively. The drumming and visual display rates were not correlated with each other (Spearman's Rank Correlation $\rho = -0.12$).

**Drumming Displays**

Mean drumming display rates (number of drumming displays per hour) in aspen each year were 5.90 (standard error [SE] = 0.99, standard deviation [SD] = 1.71), 8.31 (SE=1.22, SD=2.45), and 7.01 (SE=0.85, SD=1.89) from 2007-2009, respectively. Mean drumming display rates in conifer each year were 9.45 (SE=1.09, SD=1.88), 8.17 (SE=0.51, SD=1.13), and 5.41 (SE=1.34, SD=2.32) from 2007-2009, respectively. The intercept-only model was the top model (Table 1.2, model 1a). The interactive model including year, cover, and NND was a competitive model (Table 1.2, model 2a).

However, the relationship between the response and the model variables was not consistent, and the standard errors of the estimates for the interactions of year, cover, and NND were as large as the estimates themselves, making them less reliable. The year by cover model was also competitive, but similarly had inconsistent relationships between the model effects and variables (Fig. 1.2) as well as large standard errors. Among cumulative $AIC_c$ weights, the year parameter ranked highest (Table 1.3), which was distantly followed by cover and NND (Table 1.3). Relationships of variables with drumming displays were inconsistent for other models as well (e.g., Table 1.2, model 3a; interactions plotted in Fig. 1.2).

**Visual Display Rates**

Mean visual display rates (number of visual displays per hour of video reviewed) for all males in aspen each year were 0.003 (SE=0.003, SD=0.006), 0.04 (SE=0.009, SD=0.017), and 0.02 (SE=0.007, SD=0.015) from 2007-2009, respectively. Mean visual display rates in conifer each year were 0.02 (SE=0.006, SD=0.01), 0.01 (SE=0.008, SD=0.017), and 0.02 (SE=0.009, SD=0.015) from 2007-2009, respectively. Again, the intercept only model was the top model (Table 1.2, model 6a); no other models were competitive. The year variable had the highest cumulative $AIC_c$ weight (Table 1.3); cover and NND had cumulative $AIC_c$ weights (Table 1.3) that were relatively low and did not explain a significant amount of variation in the data.

**DISCUSSION**

Zimmerman et al. (2009) observed that male ruffed grouse in Minnesota established territories in the seemingly suboptimal conifer cover type during low density years of the grouse population cycle, despite their demonstrated affinity for aspen (Gullion and Marshall 1968, Zimmerman et al. 2009). Their observation prompted this investigation of grouse behavior to help elucidate a mechanism for the use of territories within suboptimal habitat when territories in aspen seemed available. The apparent effects that I observed of cover and NND, including interactions containing these variables, on drumming and visual display rates were inconsistent among years. For example, male visual display rates increased in aspen from 2007 to 2008, but then decreased from 2008 to 2009, even though the population size increased each year and individuals should have been experiencing increased social interactions with other grouse due to an increased population size. In addition, visual display rates were greater in conifer in 2007, less in conifer in 2008, and then greater again in 2009 (Fig. 1.2). I therefore concluded that drumming and visual display rates of male grouse were not explained by either the cover type (cover) occupied by the grouse or the proximity of males to other male grouse (i.e., NND). Several alternative explanations could explain these results. First, the sample size may not have been large enough to observe effects; however, I observed no patterns in the data to suggest this was true. Second, mate selection may have been skewed towards only a few dominant males (thus only a few males experienced interaction with conspecifics; Foster 1983), and these were, by chance, not included in my sample. While this is possible, random selection of males over

multiple years should have offset such chance sampling. Third, other factors that I did not measure may have been more important. For example, the availability of drumming structures within stands or proximity to a food source may have been more limiting than opportunities to attract potential mates. Fourth, variation in toxins among aspen clones may have influenced the locations of grouse territories. Other wildlife species preferentially feed on aspen clones with relatively lower levels of toxins (Wooley et al. 2008). It is possible that the availability of food with relatively low toxin levels may have been more limiting than opportunities to attract mates, though I did not measure aspen toxins in this study. Finally, drumming and visual display rates were not correlated, which suggested that effort spent attracting mates or deterring competitors did not necessarily result in more or fewer conspecific interactions.

Aspen had a higher carrying capacity than other cover types (Zimmerman et al. 2009) for the grouse population inhabiting this study area in 2002-2005. This pattern continued during my study when over 50% of male territories were in aspen each year (Fig. 1.1), even though aspen only comprised 19% of the area. However, the proportions of territories in both cover types (Fig. 1.1) remained remarkably similar from year to year, suggesting that conifer was not of sufficiently lower quality to preclude males from selecting it for display sites. Although conifer sites were not selected as frequently as aspen, males were probably finding sites within conifer that had an understory of appropriate structure to provide suitable display cover and that is most frequently found in aspen as suggested by Zimmerman and Gutiérrez (2008). We observed the same phenomenon as Zimmerman and Gutiérrez (2008): drumming structures within conifer

stands were often found in small inclusions of aspen within these stands.  Beaked

hazelnut (*Corylus cornuta*) is found in both conifer (Tappeiner II and John 1973) and

aspen and I often observed this woody shrub surrounding drumming structures in both

cover types (L. Berkeley pers. Obs.).  Beaked hazelnut provides understory growth within

the pine stands at Cloquet Forestry Center (Tappeiner II and John 1973) and often

provided cover for drumming structures located within red pine stands in this study.  In

addition, balsam fir is a conifer species with branches low to the ground that provides

good display cover in conifer stands.  Balsam fir was often incorporated within other

stand types on CFC, and young balsam fir seemed to provide dense, protective cover.

Finally, conifer stands may provide a less dynamic and more consistent option for

breeding sites than aspen stands because conifer logs generally decay more slowly than

hardwood logs (Bunnell and Houde 2010).  Also, because of the rapid initial growth rate

of aspen versus slow-growing conifers (Bunnell and Houde 2010), the young aspen

stands preferred by males as breeding cover probably change more rapidly than conifer

cover.  The larger fluctuations in densities of male ruffed grouse in aspen stands (larger

increase and decreases in density) relative to conifer stands observed by Zimmerman et

al. (2009) and in this study may be linked with more dynamic vegetation structure and

occurrence of drumming structures within aspen.  It may be useful for future studies to

investigate the turnover of territories within aspen relative to conifer cover types.

Based on my study, if there is a difference in quality of conifer and aspen cover

types, it manifests itself either in the specific forest stand structure used for male breeding

displays, a life stage other than breeding, or a seasonal habitat need other than breeding-

display cover of the ruffed grouse.  My study suggests that coniferous forests can serve as

breeding habitat for grouse and that this cover type does not affect their visual or

drumming display behavior.

TABLE 1.1.

List of *a priori* models predicted to influence each response variable (i.e., drumming display rate or visual display rate) of male ruffed grouse at the Cloquet Forestry Center, Minnesota, from 2007-2009.

| Model Number | Model Description |
|:---:|:---|
| 1 | Intercept Only |
| 2 | Year |
| 3 | Year * Cover[a] |
| 4 | Year * NND[b] |
| 5 | Year * Cover * NND |

[a] Cover type = aspen or conifer

[b] NND = nearest neighbor distance

TABLE 1.2.

Results of model selection for each response variable (i.e., drumming display rate or

visual display rate) for territorial male ruffed grouse at the Cloquet Forestry Center,

Minnesota from 2007-2009.

| Response Variable[a] | Model Number | Model Description | $AIC_c$[b] | $\Delta AIC_c$[c] | K[d] | $w_i$[e] |
|---|---|---|---|---|---|---|
| D | 1a | Intercept Only | 330.05 | 0 | 2 | 0.40 |
| D | 5a | Year * Cover[f] * NND[g] | 331.06 | 1.01 | 12 | 0.24 |
| D | 3a | Year * Cover | 331.75 | 1.70 | 7 | 0.17 |
| D | 4a | Year * NND | 332.67 | 2.62 | 7 | 0.11 |
| D | 2a | Year | 333.15 | 3.10 | 4 | 0.08 |
| V | 1b | Intercept Only | 97.881 | 0 | 2 | 0.60 |
| V | 3b | Year * Cover | 100.19 | 2.31 | 7 | 0.19 |
| V | 2b | Year | 100.52 | 2.64 | 4 | 0.16 |
| V | 4b | Year * NND | 102.56 | 4.68 | 7 | 0.06 |
| V | 5b | Year * Cover * NND | -[h] | | | |

[a] D = drumming display rate; V = visual display rate

[b] Akaiki's Information Criterion adjusted for small sample sizes

[c] Difference in $AIC_c$ values between model $i$ and the top-ranked model (model with the lowest $AIC_c$

   value)

[d] Number of variables

[e] Akaike weights

[f] Cover type = aspen or conifer

[g] NND = nearest neighbor distance

[h] Model could not be analyzed because it was over-parameterized.  The sample size of visual displays

   was much smaller than that of drumming displays.

TABLE 1.3.

Cumulative AIC$_c$ weights of model variables predicted to affect visual and drumming

display rates of territorial male ruffed grouse at the Cloquet Forestry Center, Minnesota

from 2007-2009.

| Model Parameter | $\sum w_i$ Drumming Display Rate | Visual Display Rate |
|---|---|---|
| Year | 0.60 | 0.40 |
| Cover[a] | 0.41 | 0.19 |
| NND[b] | 0.35 | 0.06 |

[a] Cover type = aspen or conifer

[b]NND = Nearest neighbor distance

FIGURE 1.1.

The number of male ruffed grouse territories found in aspen and conifer cover types at the Cloquet Forestry Center, Minnesota 2007-2009 (histogram) and the total population size (line graph) of males found on the study area each year. Only males in aspen and conifer cover types are shown, but the population size includes all males found on the study area in all cover types.
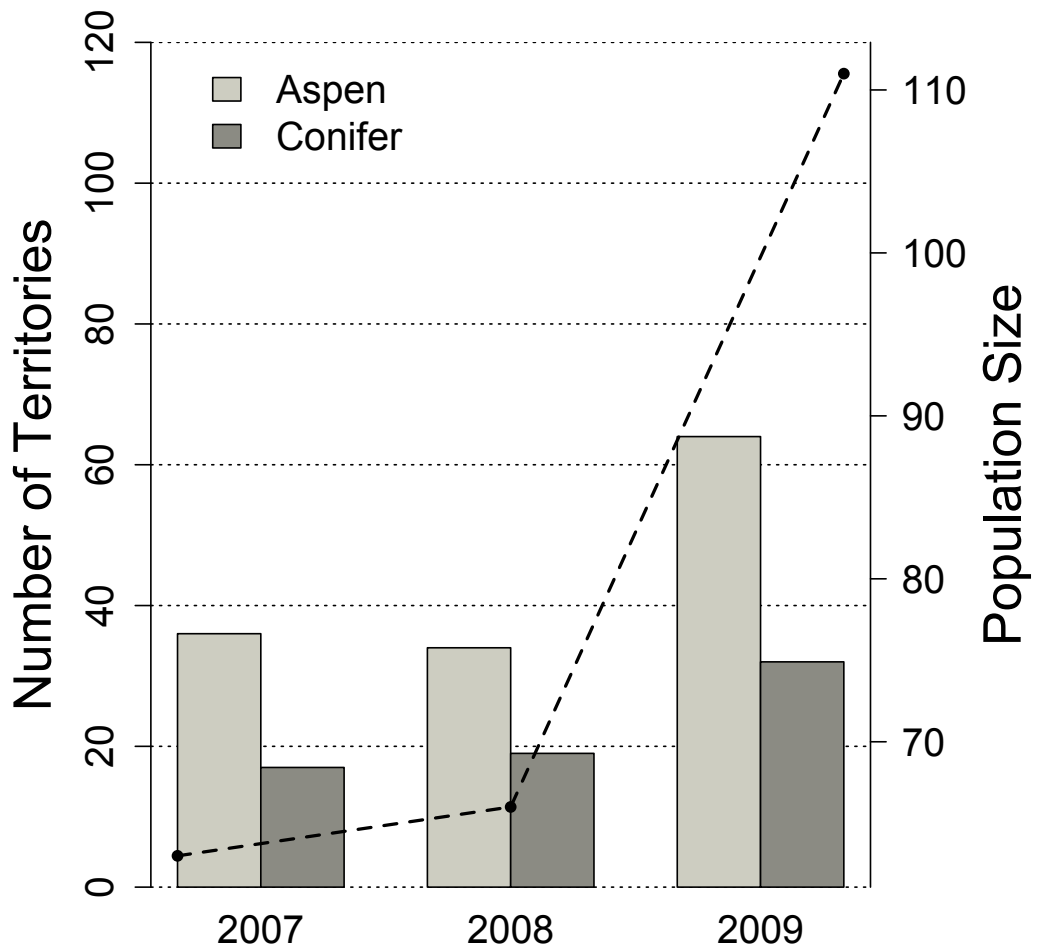
FIGURE 1.2.

Interaction plots of the effects of cover type and year on (a) visual and (b) drumming

display rates of territorial male ruffed grouse during the breeding seasons of 2007-2009

on the Cloquet Forestry Center, Minnesota.

(A)

(b)

**Male Ruffed Grouse Drumming Display Rates by Cover Type and Year**
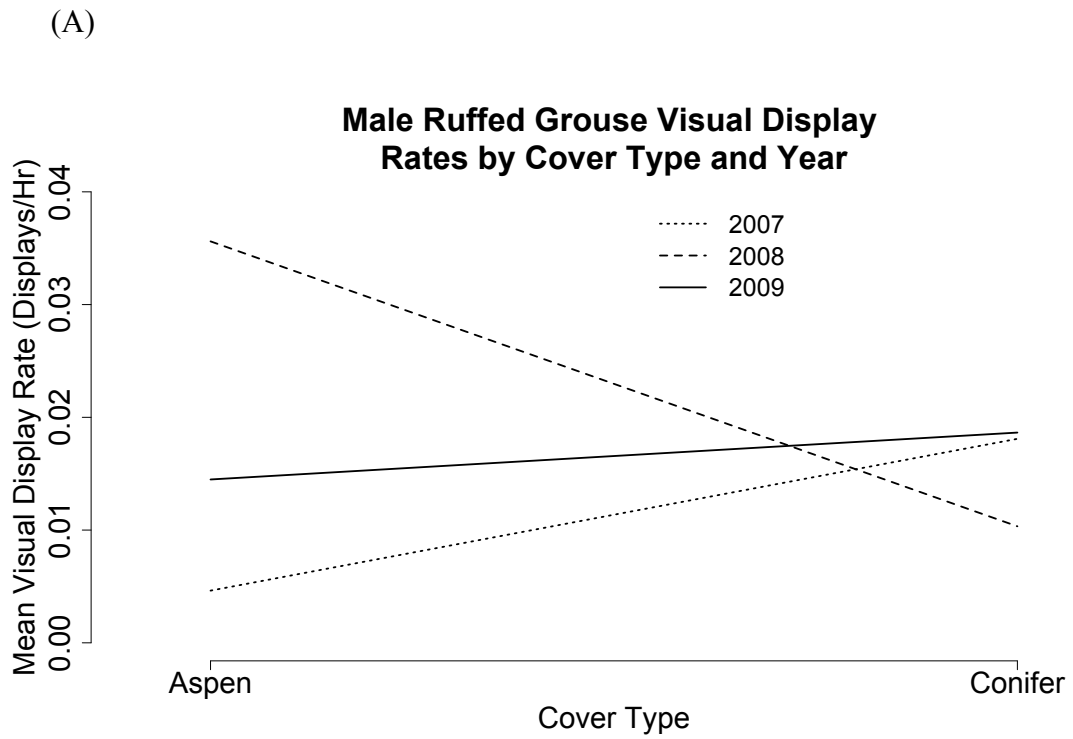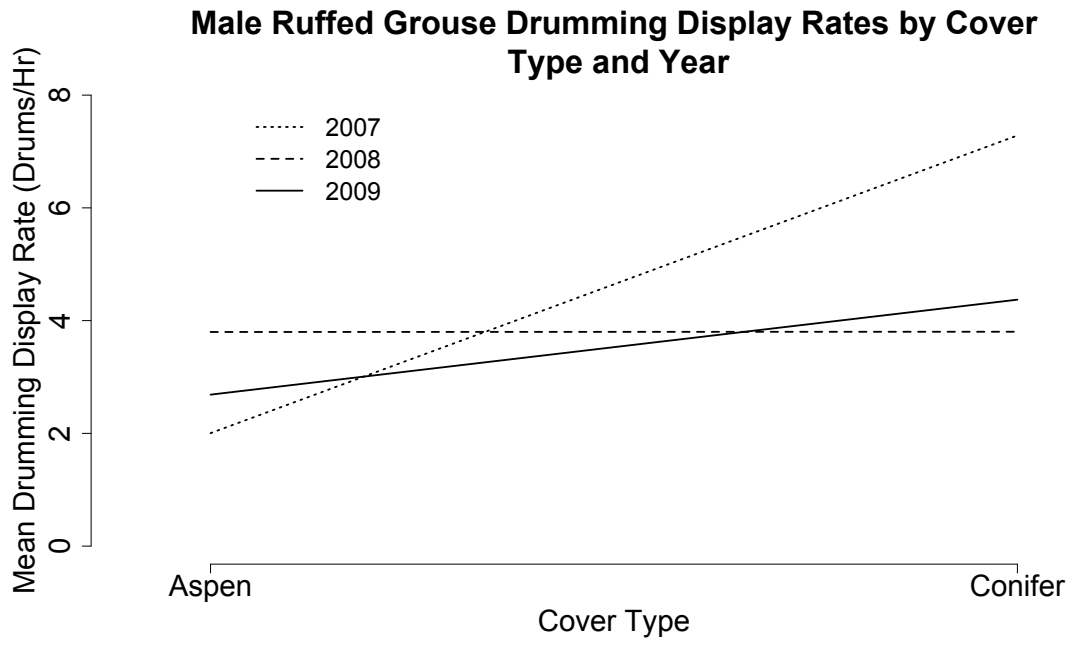
**CHAPTER 2.**


**HABITAT USE, HABITAT SELECTION, AND POPULATION DENSITY IN**

**A CYCLIC POPULATION OF RUFFED GROUSE**


**INTRODUCTION**

Studies of habitat selection in birds have long focused on use versus availability

or resource selection (Mayor et al. 2009). Linking population parameters to patterns of

habitat selection is less common in such studies because it is relatively challenging.  One

common measure of habitat quality is the density of individuals within a habitat or

landscape, although its connection to habitat quality can be uncertain (Van Horne 1983).

Regardless, understanding patterns of habitat selection in relation to population density is

of major interest to ecologists and wildlife managers because population density is a

parameter that can be monitored more easily than vital rates (Vickery et al. 1992).

Ideally, linking variation in habitat conditions to population density is best done using

experiments because these relationships can be confounded with other phenomena

(Romesburg 1981, Morris 1989).  Alternatively, linking variation in habitat conditions to

population density in species where variation in density can be reliably estimated can be

useful when experiments are not financially, legally, or logistically feasible.  Such is the

case with ruffed grouse (*Bonasa umbellus*), a species in which the males are easily

counted and many populations exhibit a cycle.  The fluctuations of numbers of

individuals during the population cycle can be viewed as a "natural experiment" when

assessing the relationship between density fluctuations and habitat conditions

(Zimmerman 2006). Moreover, the trajectory of a population cycle is often known in a

general sense (i.e., the population is either increasing or decreasing at any point in time),

which allows predictions about the relationship between habitat and population density.

Such predictions can be used to test habitat selection theory (e.g., predictions predicated

on the ideal free and ideal despotic distributions; Fretwell and Lucas 1970, Fretwell

1972) and evaluate environmental conditions that are related to population density.

Therefore, I studied a population of ruffed grouse over an entire 10-year population cycle

to explore how male population density varied by landscape composition and diversity.

The ruffed grouse (hereafter grouse) is a gallinaceous bird that lives in forests

over much of North America (Rusch et al. 2000). Throughout its range it is closely

associated with early successional forests, particularly young aspen (*Populus* spp.;

Gullion and Alm 1983, Kubisiak 1985, Atwater and Schnell 1989, Thompson III and

Dessecker 1997, Rusch et al. 2000). Past studies of grouse in northern Minnesota have

shown a strong, positive relationship between grouse density and aspen-dominated cover

types (Gullion and Marshall 1968, Zimmerman et al. 2009). The higher population

growth rates and densities of male grouse observed in aspen-dominated cover types,

particularly during the breeding season, suggest that male grouse territory selection may

be consistent with the ideal free or ideal despotic distributions (i.e., Fretwell and Lucas

1970, Fretwell 1972). However, Zimmerman et al. (2009) also have shown that grouse

use cover types that have been reported to be suboptimal habitats regardless of population

density (Zimmerman et al. 2009).

Gullion et al. (1962) examined variation in the use of cover types in relation to the density of males in a ruffed grouse population over 30 years. In addition, Zimmerman et al. (2009) studied grouse in the same location as Gullion et al. (1962), and estimated variation in density of male grouse during a decline phase of a single population cycle. These two studies provided a sound basis for framing questions about the relationship between landscape patterns and variation in male grouse population density. Gullion et al. (1962) showed that male grouse density varied by cover type, with aspen-dominated cover types having the highest density. Zimmerman et al. (2009) provided additional evidence that male grouse had higher densities in aspen-dominated cover types, but also showed that there was a higher rate of population growth in these stands relative to conifer-dominated cover types. This higher growth rate in aspen-dominated cover types suggested that aspen-dominated landscapes were superior habitats relative to conifer-dominated landscapes in their study area. Zimmerman et al. (2009) showed that male grouse densities were highest in landscapes that had a relatively high evenness of cover types relative to other landscapes. Finally, Kouffeld et al. (2013) tested this relationship in a different area in northern Minnesota. They reported that a relatively high evenness of cover types within landscapes was an important factor predicting the density of grouse in landscapes, though it was not a significant relationship as it was in Zimmerman et al. (2009). However, the relationship may have been obscured because of high male densities at the peak of the population cycle. Because these more recent studies were conducted at specific times during the cycle (declining and peak populations, respectively) rather than over an entire cycle, it was unclear if patterns of density within

landscapes remain consistent throughout the cycle. This information would be important for drawing general inferences about habitat quality for ruffed grouse and for making management recommendations. Therefore, I studied a ruffed grouse population through an entire population cycle. Specifically, I predicted that (1) the density of males will vary among cover types, (2) male grouse densities will be highest in landscapes having a relatively high evenness of cover types within landscapes, and (3) grouse will always have a higher population growth rate in aspen-dominated rather than conifer-dominated cover types regardless of the stage of the cycle.

## METHODS

### STUDY AREA

I studied male grouse at the Cloquet Forestry Center (CFC; 46˚ 31' N, 92˚ 30' W) in northern Minnesota, United States of America (USA). CFC is a 1,419-ha research forest located 36 km west-southwest of Duluth, Minnesota at 386 m above sea level. CFC is ideal for such a study because the many forestry experiments conducted here have resulted in a mosaic of cover types varying by age and size class. CFC is in the boreal forest biome, which is characterized by warm, humid summers and cold, dry winters (Tester 1997). CFC is composed of two-thirds upland cover types, such as early successional herbaceous and woody plant communities, and one-third lowland cover types such as bogs and forested wetlands. Dominant upland tree species include red pine (*Pinus resinosa*), aspen (*Populus tremuloides*), jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), and paper birch (*Betula papyrifera*).

Common lowland tree species include black spruce (*Picea mariana*), northern white cedar (*Thuja occidentalis*), tamarack (*Larix laricina*), and black ash (*Fraxinus nigra*; Cloquet Forestry Center 2006).  Beaked hazel (*Corylus cornuta*) and alder (*Alnus* spp.) were common woody shrub species in the forests.  Treeless cover types were also present on CFC and included developed areas, fields, lowland brush, upland brush, treeless wetlands.

## DRUMMING SURVEYS

Male grouse are ideal models for habitat selection studies because their density predictably fluctuates over a 10-year cycle, but, more importantly, territorial birds can be easily located.  I located grouse by the sound of their territorial announcement display, a mechanical sound called drumming produced by air rushing into a vacuum created when beating their wings against the air (Gullion 1966).  Zimmerman (2006) established 9 permanent transects at CFC in 2002 from which to locate grouse during drumming surveys.  He estimated that he and his observers had ≥0.99 probability of detecting drumming grouse within 175 m of the center line of any transect (see *A Priori* **Models**, *Landscape Scale* below).  Consequently, these survey transects were designed to be within 175 m of any upland forest stand on the study area.  Consequently, all grouse on the CFC were within a bounded transect (i.e., landscape) and were available for detection.

I conducted auditory surveys annually on 9 transects during the breeding season (April through early June) when annual drumming activity was highest (Gullion 1984,

Rusch et al. 2000). My surveys were based on a robust design (Cormack 1964, Jolly

1965, Seber 1965, Pollock et al. 1990) that included repeated surveys distributed over

three sampling periods: beginning, middle, and end of the breeding season. I made these

sampling period distinctions because grouse exhibit temporal variation in drumming

(Gullion 1966) and because the probability of detecting a male grouse increases with

multiple surveys (Zimmerman and Gutiérrez 2007). Within each sampling period, I

assumed the population to be closed to emigration, immigration, birth (in our case,

hatching does not occur until after the sampling season has ended), and death. During

each non-sampling period, I assumed the population to be open to emigration,

immigration, birth (see above), and death. Each sampling period was separated by a two-

week non-sampling (open) period. I conducted 5 surveys (one each day) on each of 3

weekly open sampling periods for a total of 15 surveys per transect during each breeding

season. I randomly selected the order in which transects were surveyed during each

sampling period. I also randomly assigned all observers to surveys with the criterion that

each observer had to survey each transect at least once during each sampling period.

Surveys began 30 min before sunrise and continued throughout the early morning (daily

peak activity time of grouse; Rusch et al. 2000). The duration of surveys depended on

the number of males detected along the route and the number of drumming structures that

were located, but increased effort on transects that had a higher density of grouse did not

affect counts (Kouffeld et al. 2013). Once a bird was heard drumming, the observer

estimated its position by compass triangulation and then stealthily approached the bird to

visually confirm its true location. The exact location of the bird was then recorded using

a global positioning system unit. Visual confirmation also allowed observers to

determine if this was the only bird drumming in the local area (i.e., sometimes birds were

located near each other or in a direct line from the initial observer position so that

auditory detection alone could result in an under-estimate of birds in the same general

area). Observers did not survey during conditions that impeded their ability to detect the

birds (e.g., heavy rain/snow or wind).

## DATA ANALYSES

Habitat selection is a hierarchical process that occurs at multiple spatial scales

(Johnson 1980, Battin and Lawler 2006, Mayor et al. 2009). Therefore, I consider two

spatial scales that should be relevant to grouse: the forest stand within which the grouse

drums (this patch is the bird's activity center, which is analogous to its territory; Gullion

1967) and the landscape, which potentially encompasses each grouse's home range as

well as multiple home ranges and many cover types). Hereafter, in my analysis I

consider the entire area of each survey transect to be a landscape within which grouse

occur.

I used information-theoretic model selection to rank *a priori* models (see *A Priori*

Models below for model descriptions and separate analyses for each habitat scale; Tables

1, 2) using Akaike's Information Criterion adjusted for small sample sizes ($AIC_c$;

Burnham and Anderson 2002). I completed all analyses using packages *LME4* version

0.999999-0 (Bates et al. 2012) and *AICcmodavg* version 1.21 (Mazerolle 2012) in

program R version 2.15.2 (R Core Team 2012). The sampling units at each spatial scale

were the forest stand at the smaller scale and the landscape at the larger scale; each sampling unit was treated as a random effect in all models to account for potential variation in the data because some characteristics that may have been unique to the sampling units were not measured during the study. My response variables at each spatial scale were Poisson-distributed counts of drumming male grouse. Therefore, I generated all models as generalized linear mixed models (GLMMs) based on a Poisson distribution with a log link and an offset. The models were offset (an argument within the glmer function that performed GLMMs in the *LME4* package) by the size of each sampling unit (in ha), thereby converting the response variable to the density (number of males per ha) of male grouse within each forest stand or landscape. I considered models competitive if they were ≤2 $AIC_c$ units from the top model (Burnham and Anderson 2002). I checked all explanatory variables for correlation prior to analysis. If variables were correlated, they were not included together in the same model but one or the other was included in separate models. I also calculated isodars to evaluate predictions about habitat quality between aspen-dominated and conifer-dominated cover types (see Isodar Analysis below).

While I calculated the coefficient of determination ($r^2$) for the top model at each spatial scale to estimate how much variation in the data is explained by these models, estimating the residual variance for mixed effect models is not straightforward if a non-Gaussian distribution is used as is the case with the GLMM structure that I used for my models (Nakagawa and Holger 2013). Also, it is not obvious what value to use for unexplained variance in the $r^2$ calculation because mixed effects models contain multiple

error terms (Nakagawa and Holger 2013). There is no widely accepted method for estimating $r^2$ for mixed effect models (Nakagawa and Holger 2013), but some techniques have emerged that minimize these issues. I used the technique by Nakagawa and Holger (2013) to calculate an $r^2_{GLMM}$ calculation for the fixed effects portion of GLMMs alone (marginal $r^2_{GLMM}$), and an $r^2_{GLMM}$ calculation for the fixed and random terms together (conditional $r^2_{GLMM}$) have been developed. The marginal and conditional $r^2_{GLMM}$ allowed determination of how much variation in the data to attribute to fixed versus random effects in the models.

### *A PRIORI* MODELS

I developed separate *a priori* models for analyses of cover types (Table 2.1) and landscapes (Table 2.2). Some of the same models were included in analyses at both spatial scales. First, I included an intercept-only (null) model to evaluate the explanatory power of the variables that I chose. Second, in several models I included a fixed effect that fit a sine wave to the data for both forest stand and landscape analyses because (1) the shape of population density versus time over multiple population cycles resembled a sine wave (Larson et al. 2003, Zimmerman et al. 2008); and (2) I predicted that forest stand use would change as a function of variation in density over the 10-year cycle because theory predicts that optimal habitats are occupied first and as density increases suboptimal habitats are used (Fretwell and Lucas 1970, Fretwell 1972). I used Year alone in some models because I predicted that some variables would interact with Year to affect male densities in cover types or on landscapes (e.g., variation in year to year density as a result of climatic conditions; Zimmerman et al. 2008). For all models, I

converted Year to a numeric variable with a mean of 0. Years with values less than zero represented years when the population was declining with the lowest value being the lowest point of the cycle, and years with values greater than zero represented years when the population was increasing with the highest value being the peak of the cycle. Designating years in this way to depict the stage of the cycle was advantageous because it reduced the number of parameters and complexity of models.

Zimmerman et al. (2008) reported that the interaction of precipitation and temperature during the winter season (1 December – 31 March each year) immediately preceding the breeding season was correlated with drumming counts. Counts of drumming males recorded during road-side drumming surveys were highest following either cold and snowy or relatively warm and dry winters and lowest during cold and dry or relatively warm and snowy winters. I used the same weather covariates in my *a priori* models to depict these weather conditions as those used by Zimmerman et al. (2008): number of days that the snow depth exceeded 15 cm (SD), the number of days with extreme low temperatures (below -15°C; $C_w$), the mean daily minimum temperature during winter ($T_w$), and interactions between SD and $C_w$ or SD and $T_w$. I used the same variables because I wanted to make direct comparisons to their research. I included these explanatory variables in models at both spatial scales. At the stand scale, models included these explanatory variables as well as those of Year, the quadratic effect of year, and forest stand (both pooled and fine-scale). At the landscape scale I modeled these variables with the quadratic effect of year as well as Shannon's Evenness Index (SEI; both pooled and fine-scale, see *Landscape Scale* below). I modeled forest stand and SEI

with weather variables because I predicted that certain cover types would be more important in years with bad winters. I also predicted that landscapes with a relatively high evenness of cover types within landscapes might allow grouse to (1) find alternative cover types for shelter from cold weather if roosting snow was not available in their preferred forest stand (Thompson III and Fritzell 1988), or (2) have access to more food options. I obtained weather data from the weather station at CFC, which was operated by the University of Minnesota.

**Cover Type Scale**

I defined forested cover types as contiguous populations of trees that were considered individual units. These individual units had a single tree species composing >66% of the stand (Smith et al. 1997) and were the sampling unit for models at this spatial scale. The mean and median forest stand sizes across CFC were 2.74 ha$^2$ and 1.57 ha$^2$, respectively ($n$ = 506 stands, SD = 4.44 ha$^2$) and ranged from 0.13-61.20 ha$^2$ (lower quartile = 0.78 ha$^2$; upper quartile = 3.22 ha$^2$).

I used two different forest stand classifications for cover types to evaluate stand structure and age associations with grouse densities; these classifications reflected fine and pooled scales. The fine-scale forest stand categories were young aspen-dominated stands (aspen stands 5-25 yrs old), mature aspen (>25 yrs old), pine (red pine or jack pine; white pine [*Pinus strobus*] and Scotch pine [*Pinus sylvestris*] were also found on the center but never composed ≥66% of any stand), mixed hardwood-conifer, northern hardwoods (birch, maple), forested wetlands (northern white cedar, tamarack, black ash),

upland conifers (mix of upland conifer species), spruce-fir (white spruce, balsam fir), and

other (developed areas, fields, lowland brush, upland brush, non-forested wetlands).  I

distinguished between young and mature aspen patches because male grouse depend on

young aspen for display habitat (Gullion and Marshall 1968, Kubisiak 1985) and mature

aspen for food (particularly during the winter; Svoboda and Gullion 1972, Thompson III

and Dessecker 1997).  I did not survey aspen stands less than five years old because trees

in these stands had not grown enough to provide overhead cover for displaying grouse,

though I did survey these stands to determine when grouse began to use them and to

ensure I was not missing displaying males.  I distinguished among conifer cover types

because they varied in structure.  For example, pines had relatively few branches near the

ground (i.e., less cover from predators or thermal protection) compared with balsam fir

and spruce.  Pines also had larger branches higher in the canopy compared with other

conifers, and northern goshawks (*Accipiter gentilis*; a primary predator of grouse*)* will

use such branches as hunting perches (Dessecker and McAuley 2001).  For coarse-scale

cover types I pooled some of the fine-scale categories (hereafter pooled cover types).

The pooled forest stand categories were the same as the fine-scale categories above

except that I pooled all age classes of aspen into one category and all species and age

classes of conifer into one category.  The resulting forest stand categories were aspen,

conifer, mixed hardwood-conifer, northern hardwoods, forested wetlands, and other

(developed areas, fields, lowland brush, upland brush, non-forested wetlands).  I

considered *a priori* models with variables including fine-scale forest stand, pooled forest

stand, and cover type shape (perimeter:area of each cover type) because models including

these variables performed best when Zimmerman et al. (2009) evaluated the relationship between stand attributes and density of male grouse while the population was declining. Hereafter I refer to aspen-dominated cover types as "aspen" and conifer-dominated cover types as "conifer" at both spatial scales.

**Landscape Scale**

I consider the bounded survey transects to be landscapes. My nine transects ranged in size from 79.25 to 253.73 ha$^2$. Transects were 350 m wide; this width was based on detection distances of observers in field tests and the size of Cloquet (Zimmerman 2006). All observers could hear grouse at least to 350 meters (Zimmerman 2006). Some transects were less than 350 m width because of topography and vegetation (e.g., surveys were not conducted in the middle of extensive marsh areas because grouse do not use these areas for displaying). Thus, when transects potentially overlapped I used the mid-point between the center lines of the two adjacent landscapes to define the landscape boundary.

Each landscape comprised a mosaic of cover types. Zimmerman et al. (2009) and Kouffeld et al. (2013) showed that landscapes having a relatively high evenness of cover types within landscapes, measured using SEI (Shannon's Evenness Index), had higher male densities during the cyclic decrease and the peak of the cyclic increase, respectively. Therefore, I considered *a priori* models with SEI calculated for both pooled (SEI$_p$) and fine-scale (SEI$_f$) forest stand classifications. I also included *a priori* models with the proportion of aspen (PA) or conifer (PC) in each landscape (Fig. 2.1). I did not consider

models that included both SEI (pooled or fine-scale) and PA or PC because PA and PC were correlated with SEI measures (see "RESULTS, Relationship Between Density and Landscapes"). However I evaluated other models that included PA or PC (Table 2.2) to determine if these variables were related to variation in grouse densities. The relative value of the aspen and conifer cover types to grouse has been of particular interest to managers because grouse have used each forest stand differently (e.g., Bump et al. 1947, Gullion and Alm 1983). Grouse have been associated with aspen where it occurs (Rusch et al. 2000), and aspen has been shown to confer greater fitness benefits to grouse (Gullion and Marshall 1968, Zimmerman et al. 2009) relative to conifers. In addition, there has been controversy over the future of forest management in the north-central states of the USA because proposals have been made to increase the proportion of conifers across the landscape, which has the potential to reduce grouse habitat. Zimmerman and Gutiérrez (2008) showed that conifer forests, in general, lack the appropriate structure to provide optimal cover for male grouse during the breeding season relative to aspen unless aspen inclusions are embedded within conifer stands.

ISODAR ANALYSIS

Zimmerman et al. (2009) conducted an isodar analysis that showed male grouse exhibited a higher growth rate in aspen versus conifer and advanced a hypothesis that the same result would be observed throughout the cycle if aspen was, indeed, better habitat (i.e., had the capacity to support a higher density of territorial males) than conifer. I tested this hypothesis by conducting an isodar analysis on grouse in aspen versus conifer

habitats during both the cyclic increase (2006-2010; Fig. 2.2a) and the entire population

cycle (2002-2011; Fig. 2.2b).  I did not test this prediction using aspen versus other cover

types because other cover types were either used only during the incline phase or had

very low density, and because the ecological value of conifers to grouse was still

uncertain (see Results, Relationship Between Density and Cover Types; Barber 1989,

Gullion 1990b, Zimmerman et al. 2009).  Isodars are graphical lines that depict either one

or two species' densities at varying population sizes in two habitats.  Theoretically,

isodars relate the spatial distribution of individuals to habitat quality based on predicted

relationships between occupied habitat and population regulation, especially under the

ideal free distribution (Morris 1988, Rosenzweig 1991, Zimmerman et al. 2009).  I used

linear regression to estimate the intercept and slope of the best-fit lines (i.e., isodars) of

the densities of males in aspen stands regressed on the densities of males in conifer stands

during the cyclic increase and throughout the entire population cycle.


**RESULTS**

**RELATIONSHIP BETWEEN DENSITY AND COVER TYPES**

During 2006-2011, the male grouse population increased for the first 4 years and

then declined for 1 year (Fig. 2.3).  This rise and decline in combination with data from

Zimmerman et al. (2009) encompassed an entire cycle.  The number of birds per stand

during this cycle ranged from 0-5.  Of the pooled cover types, aspen held the highest

male grouse densities in all years (0.12 – 0.17 males/ha during 2002-11; Fig. 2.3) except

2006 and 2011 when density was highest in northern hardwoods (0.12 and 0.13 males/ha,

respectively; Fig. 2.3). The density of males in conifer was always less than the density of males in aspen (0.02 – 0.08 males/ha during 2002-11; Fig. 2.3). Grouse densities differed among pooled cover types and among years (Table 1.3). Of the fine-scale cover types, young aspen ($\leq$25 yrs old) supported the highest densities throughout the cycle (0.10 – 0.40 males/ha during 2002-11). There was a spike in the density of male grouse in young aspen during 2009, the year immediately preceding the peak of the population cycle (Fig. 2.3). The largest changes between years in male densities occurred in aspen during the years immediately prior to and following the high peak of the cycle (2009 and 2011; Fig. 2.4).

The top-ranked model showed that densities of males in individual cover types over the entire population cycle varied among pooled cover types (young and mature aspen pooled into one "aspen" category; different conifer species pooled into one "conifer" category) and with the population cycle (modeled by fitting a sine wave to the data; Tables 2.3; Table 2.4, model 10). There were three models that appeared competitive based on $AIC_c$ values. However, these models were all essentially the same as the top model because they all included the sine function and either pooled or fine scale cover type. Two of these competitive models contained the additional variable, patch size. Upon further examination, patch size explained no additional variation in the data and is likely an erroneous result from the $AIC_c$ process (model averaged unconditional 85% CI = -17.81 - 2.84; Arnold 2010). Because of the similarities among the models and the erroneous variable, I am drawing inference from only the top model (Table 2.4, model 10). This top model had an $AIC_c$ weight of 0.27. The top model with

the other three "competitive" models (essentially embellishments of the top model) had a

total $AIC_c$ weight of 0.89 (Table 2.4, models 10, 15, 12, 17).  Thus the population cycle

(sine function fit to the data) and cover type had the most influence on male grouse

densities in cover types among the variables chosen for *a priori* models.  The fixed

effects in this top model explained only 11% of the variation in the data (marginal $r^2_{GLMM}$

= 0.11).  Variation explained by both the fixed and random effects, where the random

effect was the forest stand, was 47% (conditional $r^2_{GLMM}$ = 0.47).  Marginal habitats such

as other (developed areas, fields, lowland brush, upland brush, non-forested wetlands),

upland conifers, and forested wetlands had low densities and were mostly used toward

the peak of the incline phase of the population cycle (Fig. 2.3).  Of the pooled cover

types, conifer composed the largest proportion of cover types on CFC, followed by aspen

(Fig. 2.5).

There were 66 events during 2002-2011 that included clearing trees from road

edges, thinning stands, or clear-cutting stands on my study area.  Out of these 66 events,

there were 10 cover types affected that contained drumming structures.  There were 29

drumming structures within these 10 affected stands, several of these structures were

alternate structures before, during, and after the event (i.e., their status did not change,

and these did not represent territories).  Consequently the number of territories affected

was even smaller (each territory contains 1 primary and usually 1 to several alternate

drumming structures).  Only 1 log was a primary structure during the year of the event

(and was a primary structure before the event and remained a primary structure after the

event), and 3 were primary structures before the event and subsequently became alternate

logs following the event. There were not enough territories affected to evaluate the effects of harvest. However, when clear-cutting occurred, if aspen was the species to regenerate and there was debris in the stand (stumps and logs from clear-cutting), I did observe male grouse begin selecting territories within these areas about 5 years after logging occurred. Female grouse with broods were observed using these areas even earlier.

### RELATIONSHIP BETWEEN DENSITY AND LANDSCAPES

The number of drumming male grouse in the CFC population during the cycle ranged from 47 – 134 (Fig. 2.3), and the mean densities of males per landscape ranged from 0.04 – 0.10 males/ha (mean = 0.06 males/ha, SD = 0.04; minimum = 0 males/ha; maximum = 0.16 males/ha or 28 males per landscape). Densities varied by the evenness of fine-scale cover types within landscapes (i.e., $SEI_f$) as well as the stage of the population cycle (sine function; Table 2.5, model 10). This top-ranking model had an $AIC_c$ weight of 0.28. There were more grouse in landscapes with relatively higher evenness of cover types than landscapes with relatively lower evenness (Table 2.6). There were two competing models, both of which contained the sine function and the proportion of aspen (PA) within the landscape. However, PA and proportion of conifer were both correlated with evenness. Landscapes with higher evenness for both pooled and fine scale cover type categories also had higher proportions of aspen ($SEI_p$ ~ PA: Spearman's Rank Correlation $\rho = 0.65$, $SEI_f$ ~ PA: Spearman's Rank Correlation $\rho = 0.78$), and landscapes with lower evenness had lower proportions of conifer ($SEI_p$ ~ PC:

Spearman's Rank Correlation $\rho = -0.87$, $P < 0.0001$; $SEI_f \sim PC$: Spearman's Rank

Correlation $\rho = -0.66$).

**ISODAR ANALYSIS - HABITAT QUALITY OF ASPEN AND CONIFER FORESTS**

Zimmerman et al. 2009 showed that while male grouse densities in both aspen

and conifer increased as the entire population increased, male densities increased more in

aspen than in conifer ($\hat{\beta}_{intercept} = 0.06$, 95% CI $= 0.03 – 0.09$; $\hat{\beta}_{slope} = 3.05$, 95% CI $= 1.64$

$– 4.45$), indicating that aspen was of higher quality than conifer. Their result, observed

during the decline phase of the grouse cycle, was slightly different than my result during

the incline phase of the cyclic (Fig. 2.2a) although I found the same positive relationship.

The regression for the cyclic increase isodar of the density of males in aspen on the

density of males in conifer had a positive intercept ($\hat{\beta}_{intercept} = 0.04$, 95% CI $= -0.09 –$

$0.17$) and a slope $>1$ ($\hat{\beta}_{slope} = 2.71$, 95% CI $= 0.03 – 5.39$; Fig. 2.2a), and the regression

was $p = 0.05$ (SE $= 0.03$); the intercept in this model was not significant ($p = 0.46$, SE $=$

$0.04$) and the slope was significant ($p = 0.05$, SE $= 0.84$). When I included data for the

entire cycle, the isodar regression had a significant, positive intercept ($\hat{\beta}_{intercept} = 0.07$,

95% CI $= 0.001 – 0.149$), a slope $>1$ that was not significant ($\hat{\beta}_{slope} = 1.49$, 95% CI $= -$

$0.08 – 3.06$), and the regression was $p = 0.06$ (SE $= 0.03$; Fib. 2b). In other words, the

isodar regressions of densities of male grouse in aspen on conifer throughout a population

cycle suggest that aspen is of higher quality than conifer and that the population growth

rate for males is higher in aspen than conifer, although the relationship was weak for both

isodars and not quite significant over the entire cycle. Thus my prediction that the

relationship would strengthen as population density increased was not entirely supported.

**DISCUSSION**

A species' density varies for many reasons such as habitat quality, social interactions (i.e., dominant individuals; territorial behavior), predation or other mortality factors, prey availability, and environmental conditions that affect reproduction (Fernández-Juricic 2001). For example, population size in black-throated blue warblers (*Dendroica caerulescens*) is regulated by multiple negative feedback mechanisms which result in a reduction of population fecundity as the population size increases (Rodenhouse et al. 2003). The relationship between density and habitat quality merits further study because density is relatively easy to measure and is a commonly used indicator for habitat quality (Anderson and Gutzwiller 2005). Such a measure allows wildlife managers to evaluate the status of species' populations and their habitats in a straight-forward way. However, whether density actually reflects habitat quality can be problematic in some cases because the relationship can become decoupled because of species characteristics or environmental conditions (Van Horne 1983, Vierling 1999). Moreover, the response of individuals to changes in habitat quality may not be linear and thus not synchronized with habitat quality measures (Williams 2013). For example, Skagen and Adams (2010) showed that nest success in lark buntings (*Calamospiza melanocorys*) had a parabolic relationship to density, with nest success optimized at intermediate densities of buntings. Finally, the factors affecting density are often confounded (Van Horne 1983), or effects on density are not observable when habitat factors are measured (Williams 2013). For

example, greater sage-grouse (*Centrocercus urophasianus*) hens often exhibit fidelity to nest-site areas among years (Fischer et al. 1993). Consequently, they may show a lag effect in their response to short-term changes in habitat. Male greater sage-grouse show similar lag effects in response to habitat changes such as energy development, where lek size or occurrence may not show declines until a few years after development occurs near a lek (Walker et al. 2007). Many bird species demonstrate breeding site fidelity, and as a consequence the density of individuals at a location could reflect past rather than current habitat conditions (Rotenberry and Wiens 2009). For these reasons, using density as a surrogate for breeding habitat quality could be misleading. However, in ruffed grouse and many other species, density seems to be an appropriate indicator of habitat quality (Kubisiak 1985, Thompson III and Dessecker 1997), particularly of aspen cover types (Gullion and Marshall 1968, Gullion and Svoboda 1972, Gullion 1976, Kubisiak 1985, Zimmerman et al. 2009).

Studies of Appalachian ruffed grouse showed they used many types of cover types (Whitaker et al. 2006). Bump et al. (1947) reported that conifers were a key resource for grouse in upstate New York because it was preferred as winter cover and received more use than other types of cover types for several months of the year, even though it was avoided during the summer. In contrast, Magnus (1949) and Gullion and Marshall (1968) showed that aspen, not conifer, was the key habitat for grouse in the upper Midwest region. Thus, while the cover types used by male grouse during the breeding season have varied across their range, they are likely best defined by their structure than by their species composition.

The structural attributes of ruffed grouse habitat are well known (Bump et al. 1947, Svoboda and Gullion 1972, Gullion and Alm 1983, Kubisiak 1985, Rusch et al. 2000, Whitaker et al. 2006, Zimmerman et al. 2009) and breeding habitat is characterized by high stem densities such as occurs in early successional cover types created by clear-cutting or natural disturbance (Gullion et al. 1962, Whitaker et al. 2006, Zimmerman et al. 2007). These breeding habitats are typically young aspen in northern populations (Svoboda and Gullion 1972, Rusch et al. 2000). The cover types in which I have found grouse, primarily in young aspen stands or conifer stands with aspen inclusions, provide the dense security cover they need for drumming. This selection does not change in relation to density or the stage of a population cycle. The selection of vegetation structure rather than particular plant species is not unique to grouse—other avian species seem to select for structural characteristics during habitat selection rather than specific species (Cody 1985). For example, Henslow's sparrows (*Ammodramus henslowii*) select structural attributes rather than composition or food resources of savannas (Johnson et al. 2011). Therefore, it may be best to avoid sweeping generalities about habitat preference regarding ruffed grouse and instead evaluate grouse habitat requirements by region (Gutiérrez 2013).

**HABITAT ASSOCIATIONS THROUGHOUT A POPULATION CYCLE OF GROUSE**

Among the variables that I chose for my *a priori* models, the cover type, the estimate of the relative evenness of cover types (Shannon's Evenness Index) within landscapes where a male's territory is located, and the population cycle modeled by the

sine function were predictors within *a priori* models of grouse densities that performed the best. These results were consistent with my expectations based on both short- and long-term studies of grouse in this region that showed their affinity for aspen forests (Gullion and Marshall 1968, Rusch et al. 2000, Zimmerman et al. 2009), their affinity for landscapes with a high evenness of cover types (Zimmerman et al. 2009, Kouffeld et al. 2013), and their cyclic population dynamics (Kubisiak 1985, Zimmerman et al. 2008).

Male grouse have been shown to be territorial (Rusch and Keith 1971) and have displayed a range of dominant and sub-dominant behavior among individuals (Gullion 1967). Adult male grouse apparently will exclude juvenile males from higher quality habitats in central and southern Appalachian populations (Tirpack et al. 2010) and a northern Minnesota population (Gullion 1967). Based on this territorial behavior and predictions from habitat selection theory in relation to such behavior (i.e., theories on the ideal despotic distribution and population density limitation; Fretwell and Lucas 1970, Newton 1992), I expected male ruffed grouse densities to stabilize in aspen stands because males would establish territories and then exclude other males when the density became too high, as has been shown for red grouse (*Lagopus lagopus scoticus*; Watson and Jenkins 1968) and sharp-tailed grouse (*Tympanuchus phasianellus*; Rippen and Boag 1974). This exclusion of some individuals would likely result in a surplus of non-territorial males in the population. Although cover types other than aspen were used with increasing frequency during the cyclic increase, male ruffed grouse density in aspen never stabilized. Gullion (1967) occasionally observed non-territorial males in a ruffed grouse population at CFC. However, I did not identify non-territorial males and thus

could not determine if there was a surplus of these males.

The fact that vacant sites in aspen remained available each year, regardless of the stage of the population cycle, prompted a couple explanations for the observed density changes within and among cover types. First, male ruffed grouse densities may not have achieved a sufficiently high density in the presumptive "preferred" cover type (aspen) for males to precipitate competitive exclusion. It has been shown that population densities, even at the peak of cycles, can vary dramatically (Row et al. 2014). If grouse density during this particular cycle was not high relative to other cycle peaks, this explanation would be possible. Alternatively, weather conditions may have affected reproduction and annual recruitment of males into the breeding population (Zimmerman and Gutiérrez 2008), or weather in concert with other factors that I did not measure such as disease, predation, or food quality or availability may have influenced male density among types of cover types. Moreover, the availability of resources such as food may exhibit large annual fluctuations that affect densities (e.g., Newton 1992). Thus, annual changes of male ruffed grouse densities among cover types during the breeding season may have reflected responses to resource limitations rather than density per se. This explanation seemed reasonable because it appeared that there were always sites available in aspen regardless of the population size, and the density in aspen never stabilized. Newton (1992) suggested that this alternative seemed plausible for some forest grouse species (e.g., ruffed grouse, spruce grouse [*Dendragapus canadensis*], and blue grouse [*Dendragapus obscura*]). Lastly, variation in toxins among aspen clones may have influenced the locations of grouse territories. Other wildlife species preferentially feed

on aspen clones with relatively lower levels of toxins (Wooley et al. 2008). It is possible that grouse located their territories in areas with mature aspen of relatively low toxin levels, though I did not measure aspen toxins in this study.

I also expected male ruffed grouse to use aspen stands almost exclusively in low-density years. However, even though aspen was the most frequently used cover type (both in young and mature aspen pooled and young and mature aspen separately), male ruffed grouse used other pooled cover types even during low-density years and when sites in aspen seemed to be available (i.e., unoccupied stands that were close to birds occupying presumed low quality habitat). The presumed low quality pooled cover types that were used included conifer (pine, spruce-fir, upland conifers), forested wetlands (northern white cedar, tamarack, black ash), and other (developed areas, fields, lowland brush, upland brush, non-forested wetlands). Males may have used these cover types because there were unique qualities about these sites in terms of appropriate vegetation structure (Zimmerman and Gutiérrez 2008).

Zimmerman et al. (2009) showed that cover type shape and the fine-scale cover type classification that distinguished between young and mature aspen and among different types of conifer stands (pine, spruce-fir, upland conifers) were the best predictors of grouse densities in stands during the decline phase of a population cycle. The cover type shape variable was in two competing models in this study. However, it did not explain additional variation in the data and was determined to be an erroneous result. The top model consisting of the pooled cover type and population cycle covariates lends support to the hypothesis that different cover types affect male grouse density with

aspen supporting the highest male densities.  However, the goodness-of-fit for this model

was only 11% for the fixed effects, whereas the goodness-of-fit for both fixed and random

effect (i.e., forest stand) together was 47%.  The forest stand random effect was included

in all models to account for the potential and inherent but unmeasured characteristics

unique to each stand.  Because the variation explained in the data by the random effect

was relatively high, there are likely either other factors that were important in selection of

breeding habitat by male grouse that I did not measure or it reflected random events.

When I expanded my analyses to include landscapes, my results were more

consistent with other studies.  Similar to my study, Zimmerman et al. (2009) showed that

the estimate of the relative evenness of cover types (SEI) within landscapes was more

highly correlated with male grouse densities than other environmental variables measured

during a cyclic decline.  The SEI variable that represented cover type evenness within

landscapes was not in the top model of Kouffeld et al. (2013) as it was for this and

Zimmerman et al.'s (2009) study.  However, Kouffeld et al. (2013) studied male grouse

densities and landscape attributes at the cyclic peak when densities were highest, which

may have obscured the importance of landscape metrics because males were found in all

cover types and landscapes. Nevertheless, Kouffeld et al.'s (2013) study occurred during

only 3 years, and this study encompasses an entire population cycle.  Additionally, SEI

was in Kouffeld et al.'s (2013) competing model and still deemed an important factor

affecting grouse density.  The correlations of SEI with male grouse density in

Zimmerman et al. (2009) and Kouffeld et al. (2013) also did not explain a large amount

of the variation in their data at 28% and 18%, respectively.  However, SEI was more

important than all other habitat predictors in both studies. Competing models included the proportion of aspen, but I did not make inferences based on these because the proportion of aspen was confounded with evenness, where landscapes with higher evenness had higher proportions of aspen, and landscapes with lower evenness had lower proportions of conifer. Thus the effect of the proportion of aspen on male density could not be determined. The relationship between evenness and conifer may be a result of management goals. For example, at the Red Lake Wildlife Management Area and Beltrami Island State Forest in north central Minnesota, "landscapes managed to produce conifers for timber production lacked the spatial heterogeneity or food necessary to support high grouse densities" (Kouffeld et al. 2013). However, SEI was a better predictor of grouse density within landscapes than was the proportion of aspen, which agrees with the results from Kouffeld et al. (2013). Given the small amount of variation explained by SEI in all three studies, there must be other factors or combinations of factors that have not yet been considered but are important to breeding habitat selection by male grouse, such as fluctuations in the chemical content of aspen buds (their primary food; Jakubas and Gullion 1991), the availability of drumming structures within suitable cover, sites with suitable cover around the drumming structure, or other weather variables. Zimmerman and Gutiérrez (2008) suggested that when grouse select other cover types they are constrained by the presence of small inclusions of dense vegetation (like young aspen stands) within these cover types. These inclusions presumably provide suitable security cover that male grouse prefer (Zimmerman and Gutiérrez 2008). Alternatively, even though there seemed to be aspen sites available each year that

remained vacant, I did not know how many male grouse each cover type was capable of supporting or the annual variation in abundance or availability of resources such as food and drumming structures.

The forest stand compositions of landscapes on my study area remained relatively constant, though some thinning and logging occurred.  Thus, these events may have introduced some variation into the data that I did not quantify. Grouse may also have been sensitive to other changes within the landscape that I did not measure; the early successional habitat that they usually inhabit is time-sensitive with young vegetation constantly changing in size and structure (Tirpack et al. 2010).  Thus in addition to providing alternative cover during inclement weather or alternate food options, heterogeneous landscapes probably also provide a larger range of habitats in multiple stages of succession among which male grouse can move once their display sites lose optimal structure.

## HABITAT SELECTION THEORY AND GROUSE

Gullion and Marshall (1968) suggested that male grouse using conifer habitat will have reduced fitness compared to males using aspen because of lower survival owing to poor security cover.  They also suggested that these grouse would experience lower reproductive success because of fewer female visits.  In Chapter 1 I indirectly tested the prediction of lower reproductive success by measuring the number of interactions that a male had with other grouse because the logical prediction from Gullion and Marshall (1968) was that males occupying lower quality habitat would have fewer social

interactions (male or female) than those occupying higher quality habitat. However, I found no relationship between the interaction rates with other grouse and cover type used, suggesting that the structure of security cover was more essential for habitat selection (Rusch and Keith 1971) than social interactions and that selecting presumably low quality conifer cover types did not affect the interaction rates a male grouse had with other grouse during the breeding season.

Even though males in this study used presumed low quality cover types during the cyclic low in the population, densities were always lower in these cover types than densities in aspen regardless of the phase of the cycle. Kubisiak et al. (1980) reported similar results of cover type selection by male grouse in Wisconsin. The selection of territories in aspen by the majority of male grouse in my study population lent some support to the ideal free distribution theory (Fretwell and Lucas 1970) where individuals select the best habitats first (i.e., confer maximum fitness) and then sequentially select less optimal habitats (although I did not record the sequence in which territories were occupied) to maximize their fitness. However to make this determination, I also would have needed to quantify individuals' fitness by estimating survival or reproductive success (e.g., Sebastían-González et al. 2010). The fact that territories within seemingly ideal habitat always remained vacant, even when there was less competition for sites, suggests that male grouse may have had imperfect knowledge of the location of better sites. The grouse life history is compatible with a "bottom-up" habitat selection process (Kristan III 2006). Grouse are non-migratory and primarily ground-dwelling birds. They must move among cover types to explore and select habitats, versus a "top-down" species

that spends more time flying and can survey an area from above at a landscape scale before they select areas at a finer scale (Kristan III 2006).  A "bottom-up" approach may result in an information barrier such that individuals may fail to find optimal territories that are farther away, whereas a "top-down" approach may result in good knowledge of coarse-grained habitat features at a large-scale but cause the individual to miss particularly good patches of habitat at a finer scale (Kristan III 2006).  When male grouse have selected territories in seemingly suboptimal stands, we have observed that the microsite they have chosen within the stand has the dense understory vegetation structure to provide appropriate security cover (Rusch and Keith 1971).  This behavior of males seems to be consistent with a "bottom-up" approach to habitat selection, which may result in male grouse making "mistakes" in habitat selection (leaving what seems to be "better" territories vacant) because of imperfect knowledge of the area.  Thus a factor in male grouse territory choice is likely a trade-off between traveling longer distances to find the best territory but also increasing their risk of mortality, or remaining in known areas where they might have less ideal choices for territories but they avoid the risks associated with movement. Because male grouse are territorial, it remained possible that selection of cover types by males was also consistent with the ideal despotic distribution theory (Fretwell and Lucas 1970, Fretwell 1972).  However, I have no data to determine if males excluded each other from sites.  Therefore, the population may have behaved in a manner consistent with the ideal despotic distribution, but I could not make this determination in my study.  Future research could investigate the carrying capacity of cover types, investigate the annual variation in resources of cover types, or

experimentally test whether males excluded other males from particular cover types via addition or removal of individuals or playback experiments.

Even though I did not measure fitness of birds using different cover types, I did estimate isodars, which provided information about cover type quality as a function of relative densities of grouse in different cover types. Theoretically, isodars relate the spatial distribution of individuals to habitat quality based on predicted relationships between occupied habitat and population regulation, especially under the ideal free distribution (Morris 1988, Rosenzweig 1991, Zimmerman et al. 2009). Zimmerman et al. (2009) assessed habitat quality with an isodar analysis and showed a higher intrinsic population growth rate in aspen versus conifer stands during a cyclic decline, which suggested aspen was of higher quality than conifer. Zimmerman (2006) predicted that (1) this relationship would be maintained during an entire cycle where a range of densities could be observed, and (2) densities in aspen would show the largest increases at the start, rather than the end, of the cyclic increase. My isodar analysis using data from the entire 10-year population cycle supported the first prediction. However, contrary to Zimmerman's (2006) second prediction, the largest density fluctuations in my study (2006 –2011) occurred toward the peak of the cycle. When I considered only the density fluctuations in each habitat during the cyclic increase, the rate of density change in aspen relative to conifer was not as large. The regression was barely significant, suggesting the relationship was not very strong. However the pattern suggested by the isodar relationship could be explained by near saturation of aspen leading to more competition for resources (Rosenzweig and Abramsky 1985, Morris 1988, Rosenzweig 1991). I posit

that these males then selected suitable sites in conifer because there was less competition for resources and they had the potential to experience greater fitness than they would have experienced by staying in aspen.  The fact that there were vacant sites in aspen each year regardless of the population cycle also suggested that perhaps these presumed "available sites" were actually unsuitable in some way.  For example they may have lacked suitable drumming structures (Gutiérrez 2013) or the available food source of mature aspen may have been relatively high in toxins.  However, this is difficult to determine because male grouse densities in aspen never stabilized and I did not measure the carrying capacity of cover types or the annual changes in availability of resources.

Most theories regarding the distribution of individuals within a population among habitats focus on what happens to this distribution when densities reach their peak and there are discrepancies in an individual's fitness among habitats.  Less is known about habitat selection in unsaturated conditions (Greene and Stamps 2001).  As an alternative to the ideal free distribution, male grouse in my study (2006 – 2011) may be using social cues to aid them in selecting breeding territories (e.g., Ahlering and Faaborg 2006), making some favorable cover types crowded while leaving otherwise favorable patches unused (Stamps 1988, Skagen and Adams 2010).  Such an occurrence fits within the theoretical framework of an Allee-type ideal free distribution effects (Allee 1951, Fretwell and Lucas 1970).  A population following an Allee-type ideal free distribution experiences an increase in fitness at low to moderate population densities up to some maximum density, after which fitness quickly declines as density continues to increase (Allee 1951, Greene and Stamps 2001).  For example, Ward and Schlossberg (2004)

showed that black-capped vireos (*Calamospiza melanocorys*) settled in areas owing, in part, to the perceived presence of other black-capped vireos.  Using playback experiments Ward and Schlossberg (2004) were able to attract black-capped vireos to previously unoccupied habitats where these individuals successfully mated and returned the following year.  In this case, an individual's fitness may have been positively influenced by conspecifics when they reached certain densities because the presence of more conspecifics provided social information that reduced the costs of time and effort to evaluate habitat quality during dispersal (Greene and Stamps 2001).  These dynamics were in contrast to monotonic negative density-dependence predicted by the ideal free distribution (Fretwell and Lucas 1970, Greene and Stamps 2001).  The dispersers could have been inexperienced juveniles that relied on older males for reliable cues to habitat quality (Ahlering and Faaborg 2006).

I predict that male grouse use social information as well as vegetation structure to select breeding habitat.  For example, past grouse studies have shown that males know the locations of conspecifics because when a displaying male is removed from its territory it is often replaced within a day (or even an hour) by another male (Gullion 1967, McBurney 1989).  To test this prediction in grouse and determine the relative importance of each mechanism, experiments are needed because the spatial arrangement of resources and conspecifics are likely confounded.  For example, the density and spacing of drumming logs could be manipulated in different cover types to measure the influence of social cues from conspecifics, or playback experiments could be used to help determine settlement patterns and habitat use in different cover types. I have measured

the nearest neighbor distance among the primary drumming structures of males to evaluate whether the spatial clusters of males that I observed were because of clusters of resources (i.e., aspen cover) or males attempting to settle in close proximity to each other. However, this measure is confounded by population dynamics because density changes as a function of the cycle so nearest neighbor distances also change as a function of these changes in density.

In conclusion, the variation in density of grouse populations in my study area supports several theoretical constructs of habitat selection including the ideal free distribution and the Allee-type ideal free distribution. Future studies that employ experiments to assess settlement patterns and habitat use of males are now needed to elucidate particular mechanisms of habitat selection. In addition, experiments may be able to determine not only why males aggregate, but also to disentangle the confounding effects of resource availability versus conspecific attraction that limit inferences from observational studies (e.g., this study, Zimmerman et al. 2009, Kouffeld et al. 2013). This information will be of importance to ecologists studying the mechanisms underlying cyclic variation in ruffed grouse populations and wildlife managers who are trying to maintain high populations of this species under current and future threats such as loss or modification to their habitat due to development, climate change, or forest restoration that relies on increasing conifers on the landscape.

**MANAGEMENT IMPLICATIONS**

Managers of ruffed grouse habitat should consider maintaining more

heterogeneous landscapes at the cover type scale with aspen as a primary component of those landscapes. During all years of my study, I observed the highest densities of male grouse in aspen, and in particular in young aspen. This result reinforced earlier suggestions that managers focus on maintaining a mix of young and mature aspen types. However, the consistent use of conifer forest throughout the population cycle also suggested that conifers will provide suitable display habitat for males, assuming appropriate security cover within the conifer stand is present (Zimmerman and Gutiérrez 2008). Thompson III and Dessecker (1997) showed that conifers provided alternative thermal cover for grouse when snow roosting was not possible, but I did not investigate the role of thermal cover in this study. The tradeoff in terms of managing these two cover types will likely be that densities will be significantly lower in conifer- versus aspen-dominated landscapes (Kubisiak 1985, Thompson III and Dessecker 1997, Zimmerman et al. 2009).

TABLE 2.1.

List of *a priori* models used to predict the density of male ruffed grouse in cover types at the Cloquet Forestry Center, Minnesota, USA from 2002-2011.

| Model Number | Model Description | Prediction |
|---|---|---|
| 1 | Intercept Only | None |
| 2 | Year | + Year |
| 3 | Year + Year$^2$ | + Year + Year$^2$ |
| 4 | Sine(year) | + Sine(year) |
| 5 | PS[a] | – PS |
| 6 | Sine(year) + PS | + Sine(year) – PS |
| 7 | Sine(year) * PS | + Sine(year) * –PS |
| 8 | CP[b] | + A – C + NH – M –W – O |
| 9 | PS + CP | – SS + (A – C – M + NH –W – O) |
| 10 | Sine(year) + CP | + Sine(year) + A – C – M + NH –W - O |
| 11* | Sine(year) * CP | + Sine(year) + A – C – M + NH –W - O + +Sine(year) * (+A – C – M + NH – W – U)) |
| 12 | Sine(year) + PS + CP | + Sine(year) – PS + (A – C – M + NH –W – O) |
| 13 | CF[c] | + A$_y$ + A$_m$ – P + CF – UC – M + NH – W – O |
| 14 | PS + CF | – PS + A$_y$ + A$_m$ – P + CF – UC – M + NH – W – O |
| 15 | Sine(year) + CF | + Sine(year) + A$_y$ + A$_m$ – P + CF – UC – M + NH – W – O |
| 16** | Sine(year) * CF | + Sine(year) + A$_y$ + A$_m$ – P + CF – UC – M + NH – W – O + (Sine(year) * (+A$_y$ + A$_m$ – P + CF – UC – M + NH – W – O)) |
| 17 | Sine(year) + PS + CF | + Sine(year) – PS + A$_y$ + A$_m$ – P + CF – UC – M + NH – W – O |
| 18 | SD[d] | + SD |
| 19 | Sine(year) * SD | + Sine(year) * +SD |
| 20 | C$_w$[e] | |
| 21 | Sine(year) * C$_w$ | + Sine(year) * –C$_w$ |
| 22 | T$_w$[f] | – T$_w$ |
| 23 | Sine(year) * T$_w$ | + Sine(year) * –T$_w$ |
| 24 | C$_w$ * SD | – C$_w$ + SD + (–C$_w$ * +SD) |
| 25 | Sine(year) + C$_w$ * SD | + Sine(year) – C$_w$ + SD + (–C$_w$ * +SD) |
| 26 | T$_w$ * SD | – T$_w$ + SD + (–T$_w$ * +SD) |
| 27 | Sine(year) + T$_w$ * SD | + Sine(year) – T$_w$ + SD + (–T$_w$ * +SD) |

| Model Number | Model Description | Prediction |
|---|---|---|
| 28 | Sine(year) + $T_w$ * SD + CF | + Sine(year) − $T_w$ + SD + (−$T_w$ * +SD) + $A_y$ + $A_m$ − P + CF − UC − M + NH − W − O |
| 29 | Sine(year) + $C_w$ * SD + CF | + Sine(year) − $C_w$ + SD + (−$C_w$ * +SD) + $A_y$ + $A_m$ − P + CF − UC − M + NH − W − O |
| 30 | Sine(year) + $T_w$ * SD + CP | + Sine(year) − $T_w$ + SD + (−$T_w$ * +SD) + A − C − M + NH −W − O |
| 31 | Sine(year) + $C_w$ * SD + CP | + Sine(year) − $C_w$ + SD + (−$C_w$ * +SD) + A − C − M + NH −W − O |

[a] PS = Patch Shape (perimeter:area of cover type)

[b] CP = cover type categories pooled, including: aspen (A), conifer (C), mixed hardwood-conifer (M),

northern hardwoods (NH), forested wetlands (W), and other (O; developed areas, fields, lowland

brush, upland brush, non-forested wetlands)

[c] CF = cover type categories fine-scale, including: young aspen ($A_y$; aspen stands that are 10-25 yrs old),

mature aspen ($A_m$; >25 yrs old), pine (P), mixed hardwood-conifer (M), northern hardwoods (NH),

forested wetlands (W), upland conifers (UC), spruce-fir (SF), and other (O)

[d] SD = Snow depth; the number of days that snow depth exceeded 15 in

[e] $C_w$ = Duration of extreme cold events; the number of days below -15°C

[f] $T_w$ = Mean daily minimum winter temperature (°C)

TABLE 2.2.

List of *a priori* models used to predict the density of male ruffed grouse in landscapes at the Cloquet Forestry Center, Minnesota, from 2002-2011.

| Model Number | Model Description | Prediction |
|---|---|---|
| 1 | Intercept Only | None |
| 2 | Year | + Year |
| 3 | Year + year$^2$ | + Year + Year$^2$ |
| 4 | Sine(year) | + Sine(year) |
| 5 | $SEI_p$[a] | + $SEI_p$ |
| 6 | $SEI_f$[b] | + $SEI_f$ |
| 7 | Sine(year) + $SEI_p$ | + Sine(year) + $SEI_p$ |
| 8 | Sine(year) * $SEI_p$ | + Sine(year) * +$SEI_p$ |
| 9 | Sine(year) + $SEI_f$ | + Sine(year) + $SEI_f$ |
| 10 | Sine(year) * $SEI_f$ | + Sine(year) * +$SEI_f$ |
| 11 | PA[c] | + PA |
| 12 | PC[d] | − PC[d] |
| 13 | Sine(year) + PA | + Sine(year) + PA |
| 14 | Sine(year) * PA | + Sine(year) * +PA |
| 15 | Sine(year) + PC | +  Sine(year) − PC |
| 16 | Sine(year) * PC | +  Sine(year) − PC |
| 17 | $C_w$ * SD | − $C_w$  + SD + (−$C_w$ * +SD) |
| 18 | Sine(year) + ($C_w$ * SD) | + Sine(year) − $C_w$  + SD + (−$C_w$ * +SD) |
| 19 | $T_w$ * SD | − $T_w$ + SD + (−$T_w$ * +SD) |
| 20 | Sine(year) + ($T_w$ * SD) | + Sine(year) − $T_w$ + SD + (−$T_w$ * +SD) |
| 21 | $SEI_p$ + ($C_w$ * SD) | + $SEI_p$ − $C_w$ + SD + (−$C_w$ * +SD) |
| 22 | Sine(year) + $SEI_p$ + ($C_w$ * SD) | + Sine(year) + $SEI_p$ − $C_w$  + SD + (−$C_w$ * +SD) |
| 23 | $SEI_f$ + ($C_w$ * SD) | + $SEI_f$ − $C_w$ + SD + (−$C_w$ * +SD) |
| 24 | Sine(year) + $SEI_f$ + ($C_w$ * SD) | + Sine(year) + $SEI_f$ − $C_w$ + SD + (−$C_w$ * +SD) |
| 25 | $SEI_p$ * ($C_w$ * SD) | + $SEI_p$ − $C_w$ + SD + ($SEI_p$ * (−$C_w$ * + SD)) |
| 26 | $SEI_f$ * ($C_w$ * SD) | + $SEI_f$ − $C_w$ + SD + ($SEI_f$ * (−$C_w$ * + SD)) |
| 27 | $SEI_p$ + ($T_w$ * SD) | + $SEI_p$ − $T_w$ + SD + (−$T_w$ * +SD) |
| 28 | Sine(year) + $SEI_p$ + ($T_w$ * SD) | + Sine(year) + $SEI_p$ − $T_w$ + SD + (−$T_w$ * +SD) |
| 29 | $SEI_f$ + ($T_w$ * SD) | + $SEI_f$ − $T_w$ + SD + (−$T_w$ * +SD) |
| 30 | Sine(year) + $SEI_f$ + ($T_w$ * SD) | + Sine(year) + $SEI_f$ − $T_w$ + SD + (−$T_w$ * +SD) |
| 31 | $SEI_p$ * ($T_w$ * SD) | + $SEI_p$ − $T_w$ + SD + ($SEI_p$ * (−$T_w$ * +SD)) |
| 32 | $SEI_f$ * ($T_w$ * SD) | + $SEI_f$ − $T_w$ + SD + ($SEI_f$ * (−$T_w$ * +SD)) |

TABLE 2.3.

Fixed effects from the AIC$_c$ top-ranked generalized linear mixed model at the cover type
scale for male ruffed grouse at the Cloquet Forestry Center, Minnesota, USA from 2002-
2011: male grouse density ~ year * pooled cover type where young and mature aspen
and different conifer types are pooled (random effect = stand). The intercept represents
the aspen cover type.

| Fixed Effects | $\hat{\beta}$ [a] | SE [b] | $p$ [c] | 95% CI [d] |
|---|---|---|---|---|
| Intercept | -2.86 | 0.22 | < 2 e-16 | -3.30 – -2.43 |
| Sine(year) | 0.38 | 0.06 | < 2 e-16 | 0.27 – 0.50 |
| Cosine(year) | -0.37 | 0.06 | < 2 e-16 | 0.27 – 0.50 |
| Conifer | -1.85 | 0.28 | < 2 e-16 | -0.94 – 0.21 |
| Mixed Hardwood - Conifer | -2.76 | 0.90 | 0.0021 | -3.67 – -0.04 |
| Northern Hardwoods | -1.25 | 0.53 | 0.0191 | -3.84 – -1.67 |
| Other | -2.99 | 0.43 | < 2 e-16 | -2.13 – -0.38 |
| Forested Wetlands | -2.49 | 0.49 | < 2 e-16 | -3.99 – -2.00 |

[a] $\hat{\beta}$ = Parameter estimate

[b] SE = standard error

[c] $p$ = p-value

[d] CI = confidence interval

TABLE 2.4.

Results of model selection relating male ruffed grouse density at the cover type scale over

an entire population cycle (2002-2011) at the Cloquet Forestry Center, Minnesota, USA.

| Model Number | Model Description | $AIC_c^a$ | $\Delta AIC_c^b$ | $K^c$ | $w_i^d$ |
|---|---|---|---|---|---|
| 10 | Sine(year) + CP$^e$ | 2888.62 | 0 | 9 | 0.27 |
| 15 | Sine(year) + CF$^f$ | 2888.88 | 0.25 | 12 | 0.24 |
| 12 | Sine(year) + PS$^g$ + CP | 2889.08 | 0.46 | 10 | 0.21 |
| 17 | Sine(year) + PS + CF | 2889.56 | 0.93 | 13 | 0.17 |
| 31 | Sine(year) + $C_w^h$ * SD$^i$ + CP | 2892.88 | 4.26 | 12 | 0.03 |
| 30 | Sine(year) + $T_w^j$ * SD + CP | 2892.96 | 4.34 | 12 | 0.03 |
| 28 | Sine(year) + $T_w$ * SD + CF | 2893.17 | 4.54 | 15 | 0.03 |
| 29 | Sine(year) + $C_w$ * SD + CF | 2893.22 | 4.59 | 15 | 0.03 |
| 21 | Sine(year) * $C_w$ | 2964.83 | 76.20 | 7 | 0 |
| 23 | Sine(year) * $T_w$ | 2965.57 | 76.95 | 7 | 0 |
| 6 | Sine(year) + PS | 2968.07 | 79.44 | 5 | 0 |
| 4 | Sine(year) | 2968.31 | 79.69 | 4 | 0 |
| 7 | Sine(year) * PS | 2970.24 | 81.62 | 7 | 0 |
| 19 | Sine(year) * SD | 2971.54 | 82.92 | 7 | 0 |
| 25 | Sine(year) + $C_w$ * SD | 2972.08 | 83.46 | 7 | 0 |
| 27 | Sine(year) + $T_w$ * SD | 2972.41 | 83.78 | 7 | 0 |
| 8 | CP | 2983.34 | 94.72 | 7 | 0 |
| 9 | PS + CP | 2983.73 | 95.11 | 8 | 0 |
| 13 | CF | 2985.23 | 96.61 | 10 | 0 |
| 14 | PS + CF | 2985.69 | 97.07 | 11 | 0 |
| 3 | Year + Year$^2$ | 2991.60 | 102.97 | 4 | 0 |
| 2 | Year | 2997.47 | 108.85 | 3 | 0 |
| 24 | $C_w$ * SD | 3016.05 | 127.42 | 5 | 0 |
| 26 | $T_w$ * SD | 3018.48 | 129.85 | 5 | 0 |
| 22 | $T_w$ | 3024.04 | 135.41 | 3 | 0 |
| 20 | $C_w$ | 3026.97 | 138.34 | 3 | 0 |
| 18 | SD | 3037.52 | 148.90 | 3 | 0 |
| 5 | PS | 3055.67 | 167.05 | 3 | 0 |
| 1 | Intercept Only | 3055.92 | 167.29 | 2 | 0 |
| 11 | Sine(year) * CP | * | | | |
| 16 | Sine(year) * CF | ** | | | |

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[a] Akaiki's Information Criterion adjusted for small sample sizes

[b] Difference in $AIC_c$ values between model $i$ and the top-ranked model (model with the lowest $AIC_c$ value)

[c] Number of parameters

[d] Akaike weights

[e] CP = forest stand categories with all age classes per pooled cover type, including: aspen (A), conifer (C), mixed hardwood-conifer (M), northern hardwoods (NH), forested wetlands (W), and other (O; developed areas, fields, lowland brush, upland brush, non-forested wetlands)

[f] CF = cover type categories fine-scale (age classes within cover types represent separate categories), including: young aspen ($A_y$; aspen stands that are 10-25 yrs old), mature aspen ($A_m$; >25 yrs old), pine (P), mixed hardwood-conifer (M), northern hardwoods (NH), forested wetlands (W), upland conifers (UC), spruce-fir (SF), and other (O; developed areas, fields, lowland brush, upland brush, non-forested wetland)

[g] PS = Patch shape (perimeter:area of cover type)

[h] $C_w$ = Duration of extreme cold events (the number of days below -15°C)

[i] SD = Snow depth (the number of days that snow depth exceeded 15 in.)

[j] $T_w$ = Mean daily minimum winter temperature (°C)

* The model could be run but would not converge.

** Too many parameters, the model could not be run.

TABLE 2.5.

Results of model selection relating male ruffed grouse density at the landscape scale over

an entire population cycle (2002-2011) at the Cloquet Forestry Center, Minnesota, USA.

| Model Number | Model Description | $AIC_c$ [a] | $\Delta AIC_c$ [b] | $K$ [c] | $w_i$ [d] |
|---|---|---|---|---|---|
| 9 | Sine(year)[e] + $SEI_f$ [f] | 425.79 | 0 | 5 | 0.28 |
| 14 | Sine(year) * PA[g] | 425.90 | 0.11 | 7 | 0.27 |
| 13 | Sine(year) + PA | 426.21 | 0.41 | 5 | 0.23 |
| 7 | Sine(year) + $SEI_p$ [h] | 428.84 | 3.05 | 5 | 0.06 |
| 10 | Sine(year) * $SEI_f$ | 429.41 | 3.61 | 7 | 0.05 |
| 30 | Sine(year) + $SEI_f$ + $T_w$ [i] * $SD$ [j] | 430.23 | 4.43 | 8 | 0.03 |
| 15 | Sine(year) + PC[k] | 430.23 | 4.44 | 5 | 0.03 |
| 24 | Sine(year) + $SEI_f$ + $C_w$ [l] * SD | 430.83 | 5.04 | 8 | 0.02 |
| 8 | Sine(year) * $SEI_p$ | 433.22 | 7.43 | 7 | 0.01 |
| 28 | Sine(year) + $SEI_p$ + $T_w$ * SD | 433.28 | 7.48 | 8 | 0.01 |
| 22 | Sine(year) + $SEI_p$ + $C_w$ * SD | 433.82 | 8.02 | 8 | 0.01 |
| 16 | Sine(year) * PC | 434.47 | 8.67 | 7 | 0 |
| 4 | Sine(year) | 435.20 | 9.40 | 4 | 0 |
| 20 | Sine(year) + $T_w$ * SD | 438.81 | 13.01 | 7 | 0 |
| 18 | Sine(year) + $C_w$ * SD | 439.78 | 13.98 | 7 | 0 |
| 3 | Year + Year$^2$ | 457.85 | 32.06 | 4 | 0 |
| 2 | Year | 462.28 | 36.48 | 3 | 0 |
| 23 | $SEI_f$ + $C_w$ * SD | 478.20 | 52.41 | 6 | 0 |
| 21 | $SEI_p$ + $C_w$ * SD | 483.14 | 57.35 | 6 | 0 |
| 26 | $SEI_f$ * $C_w$ * SD | 484.19 | 58.39 | 9 | 0 |
| 29 | $SEI_f$ + $T_w$ * SD | 486.53 | 60.73 | 6 | 0 |
| 25 | $SEI_p$ * $C_w$ * SD | 488.49 | 62.70 | 9 | 0 |
| 27 | $SEI_p$ + $T_w$ * SD | 490.12 | 64.33 | 6 | 0 |
| 32 | $SEI_f$ * $T_w$ * SD | 492.18 | 66.38 | 9 | 0 |
| 17 | $C_w$ * SD | 494.12 | 68.32 | 5 | 0 |
| 31 | $SEI_p$ * $T_w$ * SD | 495.25 | 69.46 | 9 | 0 |
| 6 | $SEI_f$ | 496.78 | 70.99 | 3 | 0 |
| 5 | $SEI_p$ | 499.16 | 73.37 | 3 | 0 |
| 12 | PC | 500.57 | 74.77 | 3 | 0 |
| 19 | $T_w$ * SD | 504.85 | 79.05 | 5 | 0 |
| 11 | PA | 516.94 | 91.14 | 3 | 0 |
| 1 | Intercept Only | 517.91 | 92.12 | 2 | 0 |

[a] Akaiki's Information Criterion adjusted for small sample sizes

[b] Difference in $AIC_c$ values between model $i$ and the top-ranked model (model with the lowest $AIC_c$

   value)

[c] Number of parameters

[d] Akaike weights

[e] Sine(year) = sin((2*pi*year)/10), cos((2*pi*year)/10); pi = 3.1416; 10 represents the 10 year grouse

   cycle

[f] $SEI_f$ = Shannon's Evenness Index calculated using pooled forest stand categories: aspen (A), conifer

   (C), mixed hardwood-conifer (M), northern hardwoods (NH), forested wetlands (W), and other

   (O; developed areas, fields, lowland brush, upland brush, non-forested wetlands)

[g] PA = Proportion of aspen

[h] $SEI_p$ = Shannon's Evenness Index calculated using fine-scale forest stand categories: young aspen ($A_y$;

   aspen stands that are 10-25 yrs old), mature aspen ($A_m$; >25 yrs old), pine (P), mixed hardwood-

   conifer (M), northern hardwoods (NH), forested wetlands (W), upland conifers (UC), spruce-fir

   (SF), and other (O; developed areas, fields, lowland brush, upland brush, non-forested wetlands)

[i] $T_w$ = Mean daily minimum winter temperature (°C)

[j] SD = Snow depth (the number of days that snow depth exceeded 15 in.)

[k] PC = Proportion of conifer

[l] $C_w$ = Duration of extreme cold events (the number of days below -15°C)

TABLE 2.6.

Fixed effects from the $AIC_c$ top-ranked generalized linear mixed model at the landscape scale for male ruffed grouse at the Cloquet Forestry Center, Minnesota, USA from 2002-2011: male grouse density ~ year + year$^2$ + SEI$_f$ (random effect = landscape).

| Fixed Effects | $\hat{\beta}$ [a] | SE [b] | $p$ [c] | 95% CI [d] |
|---|---|---|---|---|
| Intercept | -6.37 | 0.79 | < 0.0001 | -7.97 – -4.76 |
| Sine(year/10)sin[e] | 0.32 | 0.05 | < 0.0001 | 0.22 – 0.43 |
| Sine(year/10)cos[e] | -0.33 | 0.05 | 0.0074 | -0.44 – -0.22 |
| SEI$_f$ | 4.19 | 0.97 | < 0.0001 | 2.22 – 6.16 |

[a] $\hat{\beta}$ = Parameter estimate

[b] SE = standard error

[c] $p$ = p-value

[d] CI = confidence interval

[e] Sine(year) function that was fit to the data = sin((2*pi*year)/10), cos((2*pi*year)/10); pi = 3.1416; 10 represents the 10 year grouse cycle

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FIGURE 2.1.

The proportion of aspen and conifer pooled cover types within each landscape on the

Cloquet Forestry Center, Minnesota, USA.

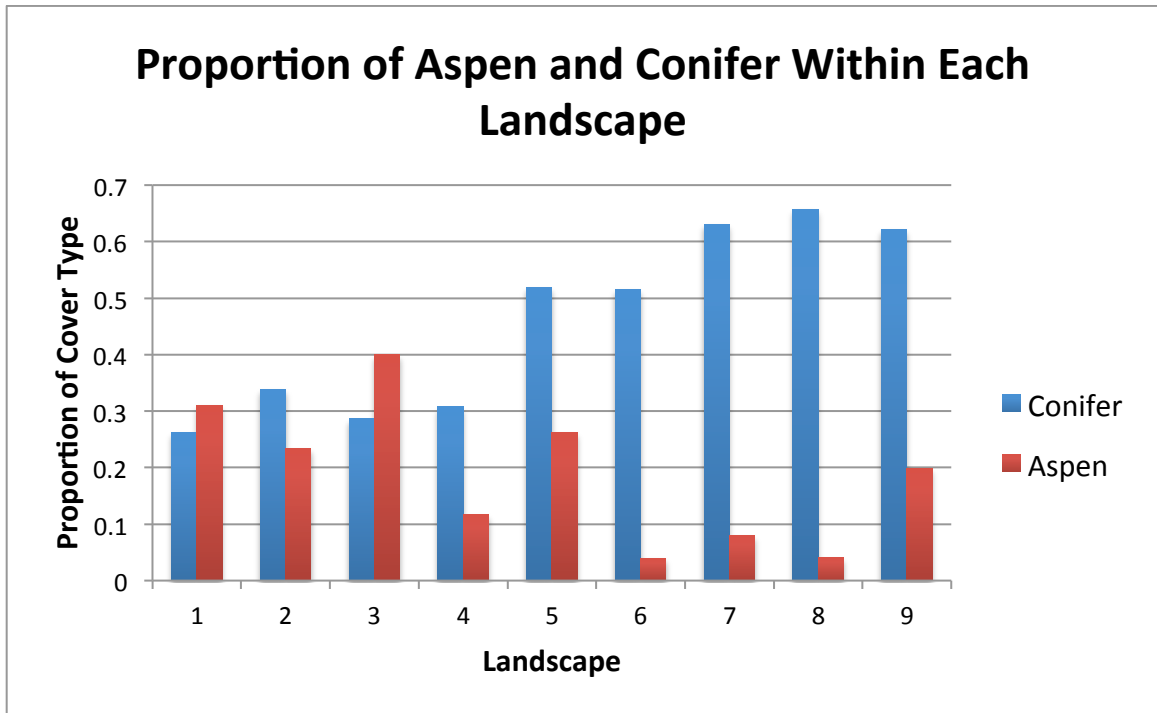FIGURE 2.2.

The mean density of drumming male ruffed grouse in aspen regressed on the mean density of males in conifer forests at the Cloquet Forestry Center, Minnesota, USA during the (a) cyclic increase from 2006-2010 and (b) entire cycle from 2002-2011. The line represents the estimated regression line of the density of males in aspen on the density of m conifer forests from observed data.

(a)
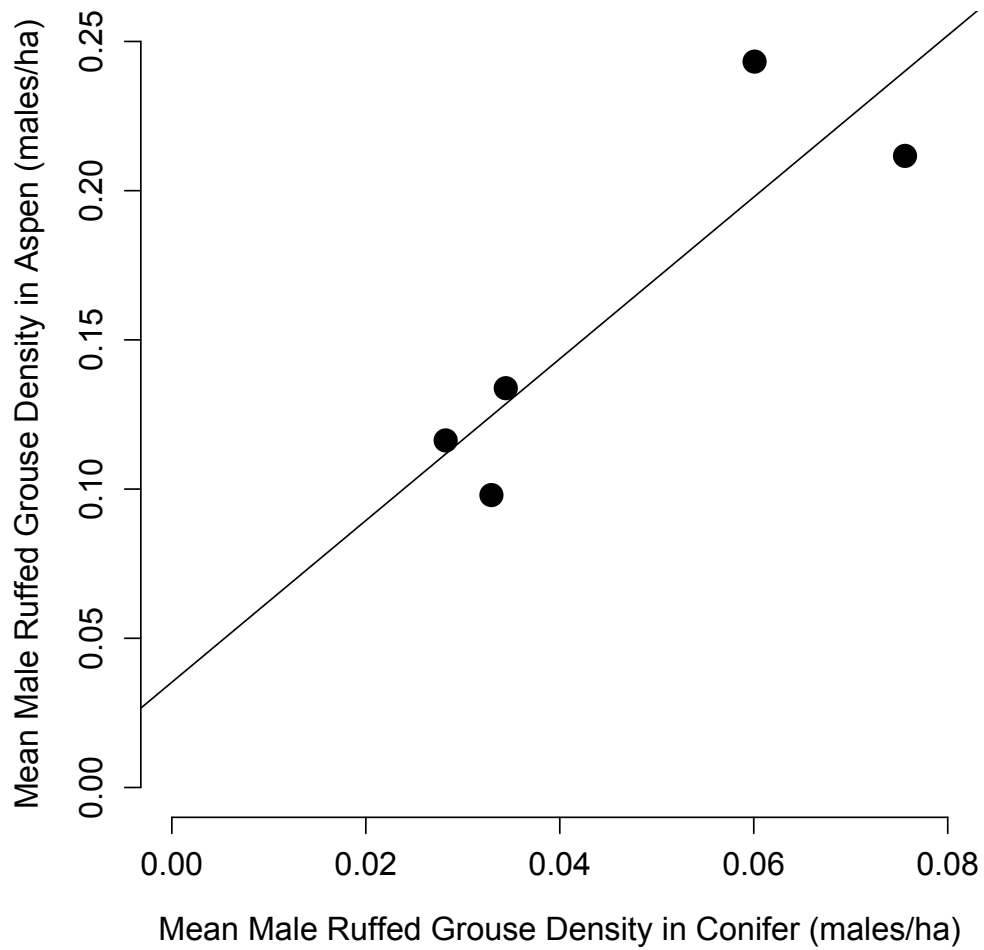
FIGURE 2.3.

The density of male ruffed grouse per pooled cover type each year (left, y-axis) plotted

with the number of males detected in the population each year (right y-axis) at Cloquet

Forestry Center, Minnesota, USA from 2002-2011.
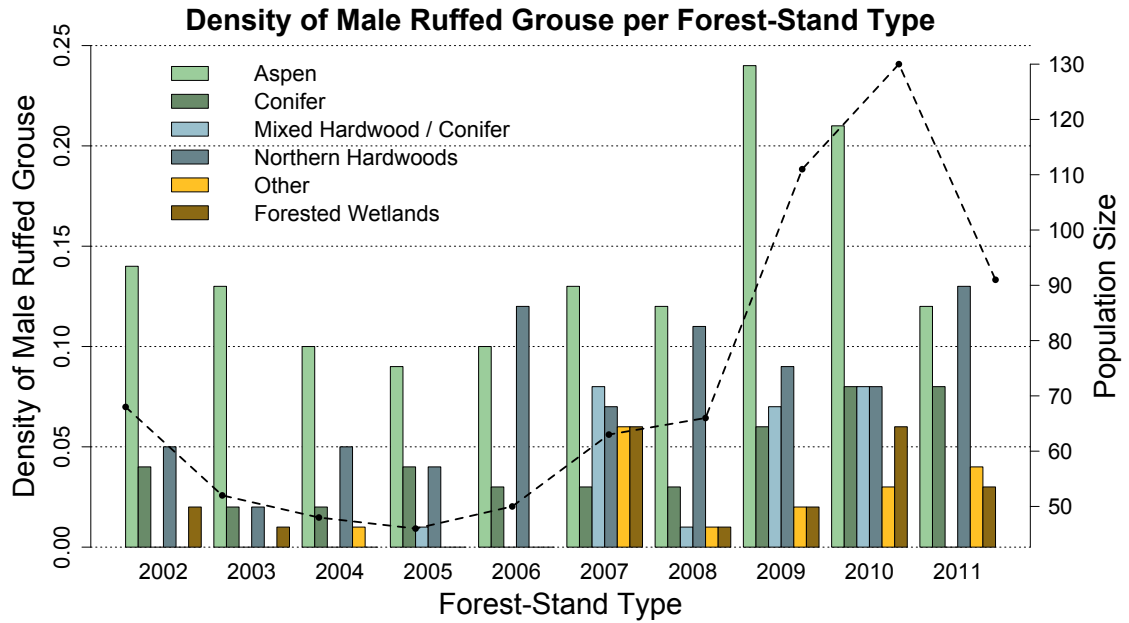
FIGURE 2.4.

The rate of change in the mean ruffed grouse density in cover types within each pooled

cover type at the Cloquet Forestry Center, Minnesota, USA from 2002-2011. All

forested cover types are represented by tree species that compose ≥66% of the entire

forest stand. Pooled cover types represent all cover types within broad classifications that

encompass multiple age classes or species that are closely related (e.g. pine stands are

classified into the conifer cover type). A = aspen; C = conifer; M = mixed hardwood-

conifer; NH = northern hardwoods; O = other (developed areas, fields, lowland brush,

upland brush, non-forested wetlands); W = forested wetlands.

FIGURE 2.5.

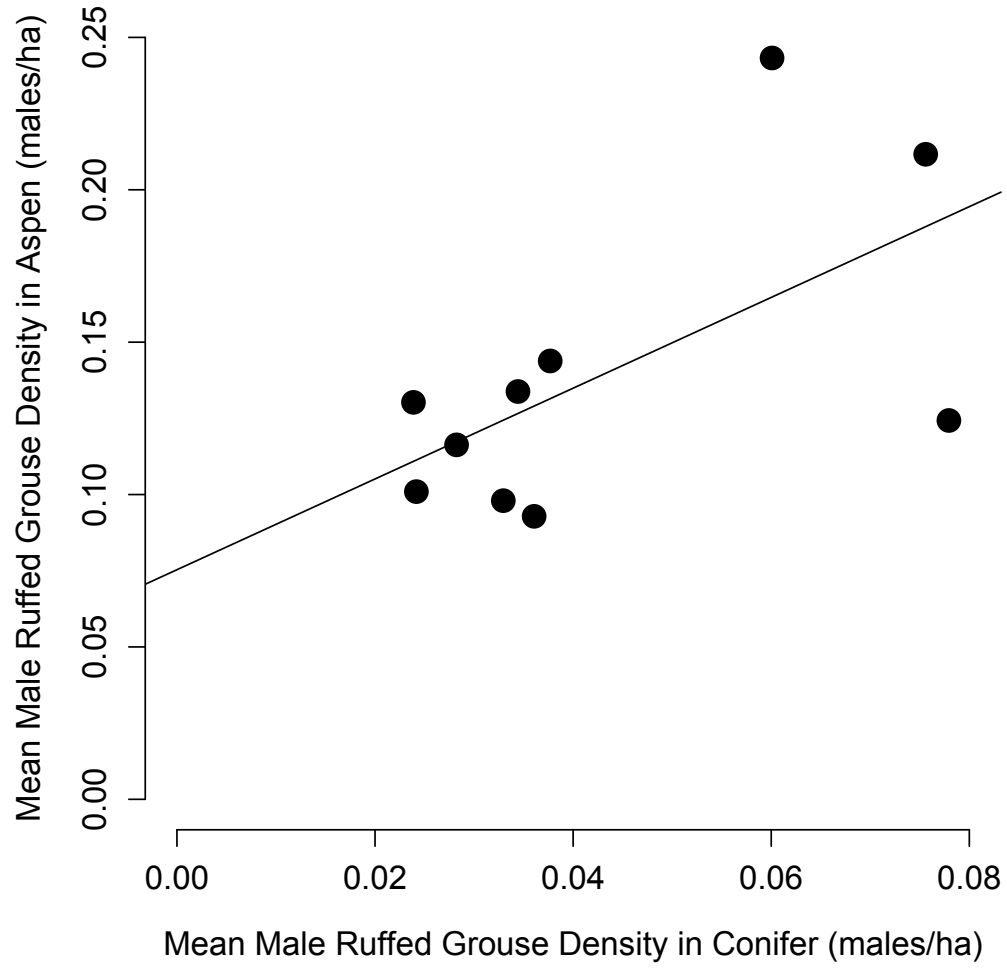The proportion of cover types in each pooled cover type on the Cloquet Forestry Center, Minnesota, USA. The proportion of cover types in each pooled forest stand type. All forested cover types are represented by tree species that compose ≥66% of the entire forest stand. Pooled cover types represent all cover types within broad classifications that encompass multiple age classes or species that are closely related (e.g. pine stands are classified into the conifer cover type). A = aspen; C = conifer; M = mixed hardwood-conifer; NH = northern hardwoods; O = other (developed areas, fields, lowland brush, upland brush, non-forested wetlands); W = forested wetlands.
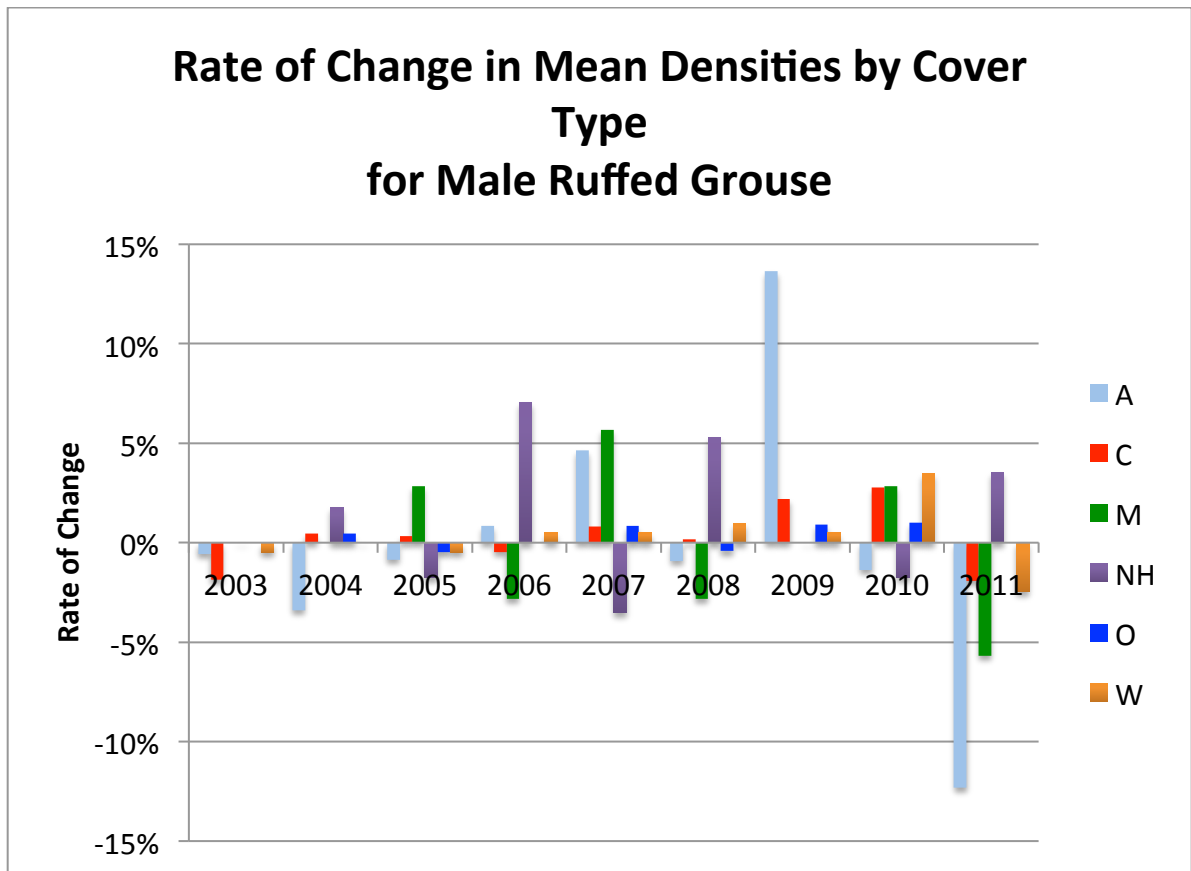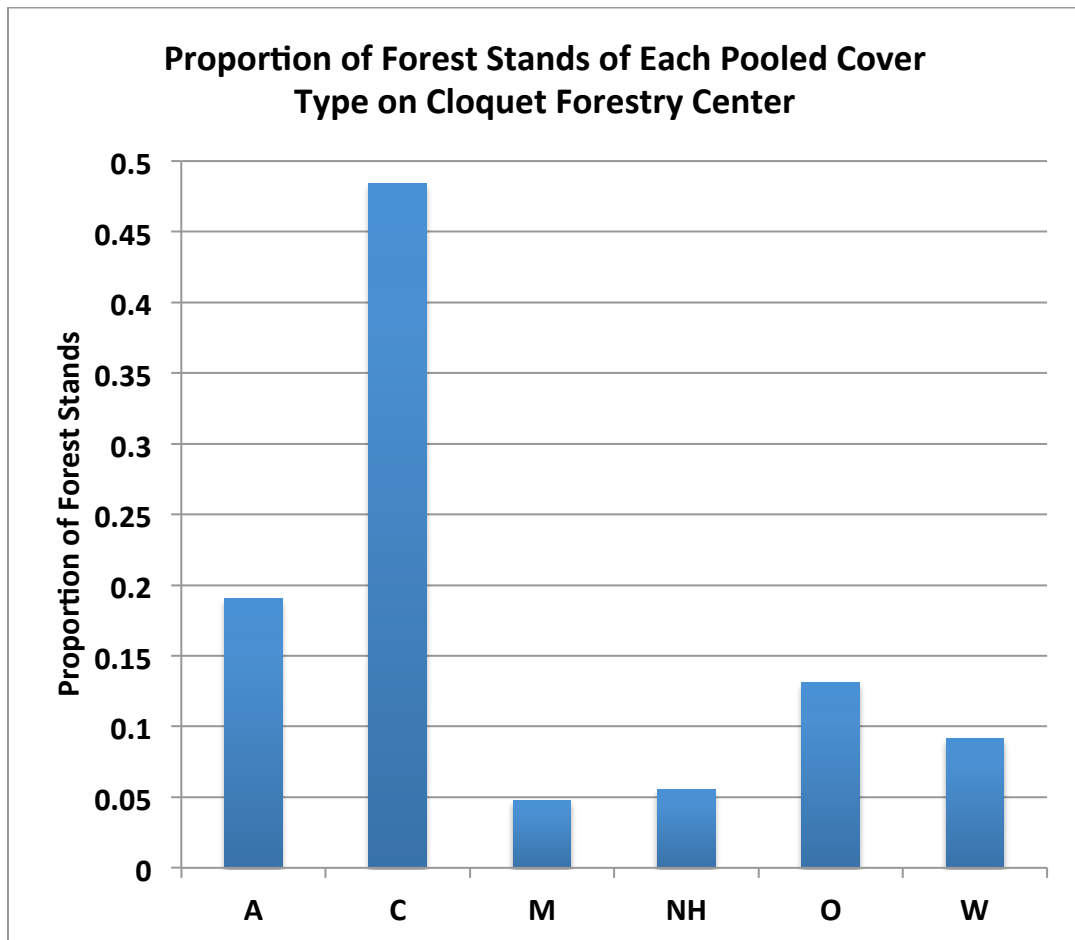


Proportion of Forest Stands of Each Pooled Cover Type on Cloquet Forestry Center

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