

8-2017

# Survival, Harvest, and Drumming Ecology of Ruffed Grouse in Central Maine, USA

Samantha Davis

University of Maine, samantha.davis2@maine.edu

Follow this and additional works at: <https://digitalcommons.library.umaine.edu/etd>



Part of the [Environmental Sciences Commons](#), and the [Population Biology Commons](#)

---

## Recommended Citation

Davis, Samantha, "Survival, Harvest, and Drumming Ecology of Ruffed Grouse in Central Maine, USA" (2017). *Electronic Theses and Dissertations*. 2784.

<https://digitalcommons.library.umaine.edu/etd/2784>

This Open-Access Thesis is brought to you for free and open access by DigitalCommons@UMaine. It has been accepted for inclusion in Electronic Theses and Dissertations by an authorized administrator of DigitalCommons@UMaine. For more information, please contact [um.library.technical.services@maine.edu](mailto:um.library.technical.services@maine.edu).

**SURVIVAL, HARVEST, AND DRUMMING ECOLOGY OF RUFFED GROUSE IN  
CENTRAL MAINE, USA**

By

Samantha Davis

B.S. New Mexico State University, 2012

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Wildlife Ecology)

The Graduate School

The University of Maine

August 2017

Advisory Committee:

Erik Blomberg, Assistant Professor of Wildlife Ecology, Advisor

Brian Olsen, Associate Professor of Biology and Ecology

Alessio Mortelliti, Assistant Professor of Wildlife Ecology

Brad Allen, Wildlife Biologist and Bird Group Leader

© 2017 Samantha Davis

# **SURVIVAL, HARVEST, AND DRUMMING ECOLOGY OF RUFFED GROUSE IN CENTRAL MAINE, USA**

By Samantha Davis

Thesis Advisor: Dr. Erik Blomberg

An Abstract of the Thesis Presented  
in Partial Fulfillment of the Requirements for the  
Degree of Master of Science  
(in Wildlife Ecology)  
August 2017

Understanding population dynamics and how species interact with their environment are important components for conservation and management. Ruffed grouse (*Bonasa umbellus*) are a widely distributed and common game bird in North America and are considered an important economic and cultural icon in Maine. Although they are a well-studied species, there has been little research focused on ruffed grouse population dynamics and habitat relationships in Maine. My thesis aims to improve this knowledge gap by focusing on research related to survival and harvest of ruffed grouse, as well as male ruffed grouse resource selection at breeding display sites. Ruffed grouse are generally considered abundant in Maine, but there is a lack of state-specific knowledge of their survival and harvest rates to inform harvest management. To address this component we estimated seasonal and annual survival rates, harvest rates, and documented cause-specific mortality of 248 radio-marked ruffed grouse at two study areas in central Maine from 2014 –2016. We used nest survival models implemented in Program MARK to evaluate sources of spatial, temporal, and individual variation that may affect survival and harvest. Our results showed survival was lowest during the month of October and during winter, and adult ruffed grouse had a higher survival probability than juveniles throughout the year ( $\beta -0.49 \pm 0.15$

SE). Harvest rates were greater in a state owned Wildlife Management Area, and were lower at our study area comprised of commercially-managed private forest ( $\beta=0.72 \pm 0.38$  SE). Pooled across all years and study areas, the ruffed grouse harvest rate was 0.16 (95% CI = 0.14-0.18). Our results are comparable to other range-wide studies, and suggest that ruffed grouse hunting regulations in Maine produce rates of harvest that are consistent with sustainable population management.

Resource selection reflects behavioral choices that species make at different levels within their environment, but the fitness consequence of these choices are not always well understood. We evaluated habitat selection at breeding display sites, and the effects on breeding behavior, of male ruffed grouse in central Maine during April and May 2015–2016. We used resource selection functions (RSFs) that took the form of generalized linear models to compare habitat characteristics at used display locations ( $n=72$ ) with those at available locations ( $n=144$ ), and we further assessed how selected habitat features from the RSFs were associated with three drumming display characteristics; drumming rate, and wing beat rate. We used Akaike's Information Criterion to assess model support and selection. We found that male ruffed grouse selected drumming locations with high total stem density ( $\beta=0.52$ , 95% CI= 0.22-0.82), as well as high conifer stem density within 5m from the display stage ( $\beta= 0.46$ , 95% CI= 0.17-0.75). However we did not find that these same variables were associated with drumming behaviors, suggesting no effect of habitat selection on breeding display behavior. Understanding habitat selection and the possible fitness consequences of those selection choices will allow managers to identify areas of critical habitat needed to further benefit the species.

## ACKNOWLEDGMENTS

I have been fortunate to have met and built relationships with many smart, talented, and wonderful people during my time at the University of Maine. I am grateful to Dr. Erik Blomberg for giving me the opportunity and accepting me as his first graduate student. He has provided me unwavering guidance, support, and encouragement throughout my M.S. program, to which I will always be grateful. Thank you Erik, for all of your support, I will never be able to express to you how much this opportunity has meant to me and how much I have valued you as a mentor. I would like to thank my committee members: Dr. Brian Olsen, Dr. Alessio Mortelliti, and Brad Allen for all of their guidance, support, patience, and feedback on this thesis. I am grateful for their willingness to assist me throughout this process despite everyone's busy schedules. It has been an absolute pleasure working with each and every one of you and I am grateful to have a committee and advisor that have provided me with exceptional knowledge and skills throughout this process.

I would like to thank the faculty, staff, and fellow graduate students from the Department of Wildlife, Fisheries, and Conservation Biology at the University of Maine for all of their support throughout this process, especially members of the Blomberg lab (Joelle Mangelinckx, Brian Allen, Joel Tebbenkamp, Sabrina Morano, Berlynnna Heres, Marie Martin, and Douglas Munn) for their assistance in the field, and in the lab. I would like to particularly extend a special thank you to Ellie how has been my partner in crime from the start of this project, I don't know how I would have survived without you! Thank you to my exceptional technicians and volunteers (Douglas Munn, Jordan Rabon, Anthony Kroeger, Brittany Currier, Steve Dunham, Tess Howard, Nicole Keefner, Lauren Dolinski, Zackary Beaudry, Dan Bailey, Caitlin Gunn, Shannon Thomas, Cody Wickett, and Graham Cole) who helped me in many ways during my

three years of field work. I am so grateful for their hard work and dedication to this project which would not have been possible without them. I would like to thank my family particularly my mom Leslie Musselmann, my dad Kenny Brown, and my husband Tyler Davis for all of their unwavering support during this process which has allowed me to reach this point in my career.

I thank the organizations and individuals that collaborated on this project. I thank Chris Dyer, Jeff Beach and Shawn Haskell of the Department of Inland Fisheries and Wildlife for their collaboration on this project, and especially Kelsey Sullivan and Brad Allen for all of their help in the field, guidance, and insight during project meetings. I thank David Cole, Todd Massey, and John Bryant of American Forest Management, Pam Wells of Wells Farm, and Nancy Sferra and the Maine Field Office of The Nature Conservancy for land access and accommodations. This research was funded by the Maine Agricultural and Forest Experiment Station, the Federal Aid in Wildlife Restoration Act, and the Maine Department of Inland Fisheries and Wildlife.

## TABLE OF CONTENTS

ACKNOWLEDGMENTS .....	iii
LIST OF TABLES .....	vii
LIST OF FIGURES.....	viii
<b>1. SURVIVAL AND HARVEST OF RUFFED GROUSE IN CENTRAL MAINE, USA .....</b>	<b>1</b>
Abstract.....	1
Introduction.....	2
Study Area .....	4
Field Methods.....	5
Trapping.....	5
Analytical Methods .....	7
Seasonal and Annual Survival.....	7
Weekly and Cumulative Harvest .....	9
Results .....	10
Discussion.....	18
Management Implications.....	25
<b>2. SELECTION OF DRUMMING LOCATIONS BY MALE RUFFED GROUSE AND EFFECTS ON DRUMMING BEHAVIOR IN CENTRAL MAINE, USA.....</b>	<b>26</b>
Abstract.....	26
Introduction.....	27
Methods .....	30
Study Area.....	30
Display Locations .....	30
Vegetation Sampling.....	31
Analytical Methods .....	33
Display Stage Selection .....	33

Acoustic Recordings .....	34
Results .....	36
Discussion.....	40
REFERENCES.....	46
BIOGRAPHY OF THE AUTHOR .....	51

## LIST OF TABLES

Table 1.1.	Ruffed grouse mortality.....	12
Table 1.2	Weekly survival model results.....	13
Table 1.3	Monthly survival probabilities of ruffed grouse.....	15
Table 1.4	Weekly harvest model results.....	16
Table 2.1	Resource selection function model results.....	36
Table 2.2	Display behavior model selection.....	40

## LIST OF FIGURES

Figure 1.1	Cumulative harvest rates.....	11
Figure 1.2	Ruffed grouse monthly survival throughout the year.....	14
Figure 1.3	Survival and harvest of ruffed grouse.....	17
Figure 2.1	Resource selection function graphs.....	37
Figure 2.2	Wing beats differences between study areas.....	38
Figure 2.3	Drumming display scatterplots.....	39

## CHAPTER 1

### SURVIVAL AND HARVEST OF RUFFED GROUSE IN CENTRAL MAINE, USA

#### Abstract

Understanding population dynamics is central to population management, particularly for game species that experience mortality in the form of harvest, in addition to non-harvest mortality that may or may not be anthropogenic in nature. Ruffed grouse (*Bonasa umbellus*) are a widely distributed and common game species in North America that have experienced population declines along their southern range margins, including portions of New England. In the state of Maine ruffed grouse are generally considered abundant, but there is a lack of state-specific knowledge of ruffed grouse survival and harvest rates to inform harvest management. We estimated seasonal and annual survival rates, harvest rates, and documented cause-specific mortality of 248 radio-marked ruffed grouse at two study areas in central Maine from 2014 – 2016. We used Program MARK to evaluate sources of spatial, temporal, and individual variation that may affect ruffed grouse survival and harvest. Survival was lowest during the month of October and during winter, and adult ruffed grouse had a higher survival probability than juveniles throughout the year ( $\beta -0.49 \pm 0.15$  SE). Harvest rates were greater in a state owned Wildlife Management Area, and were lower within a commercially-managed private forest that was open to public hunting ( $\beta=0.72 \pm 0.38$  SE). Harvest results suggest harvest was greatest at the beginning of the hunting season (Oct), and was lower latter in the season (Nov and Dec). Pooled across all years and study areas, the ruffed grouse harvest rate was 0.16 (95% CI = 0.14-

0.18). Our results are comparable to other range-wide studies, and suggest that current hunting regulations for ruffed grouse in Maine are consistent with sustainable population management.

### **Introduction**

Survival is a fundamental population process, and knowledge of factors that influence survival is important for understanding species' population dynamics (Lande 1988, Seather and Bakke 2000, Sandercock 2006). Survival may be temporally dynamic (Sandercock et al. 2011), may change spatially (Rolland et al. 2010), or may vary among individuals (Hannon and Martin 2006, Rolland et al. 2010). Individuals may be exposed to multiple mortality risks that influence survival, including those associated either directly (e.g. hunting) or indirectly (e.g. increased exposure to predators) with humans, as well as sources that are not anthropogenic in nature (Lindström 1994). Determining cause-specific mortality allows partitioning of variation in survival among competing risks, which can be important for population management (Rolland et al. 2010). This may be particularly true of game species, where individuals experience anthropogenic mortality associated with recreational hunting in addition to other sources, and management strategies must address both harvest and non-harvest mortality (Seather and Bakke 2000, Rolland et al. 2010, Blomberg et al. 2013).

Among North American upland gamebirds, ruffed grouse (*Bonasa umbellus*) have one of the larger distributions, extending across the northern United States and Canada as well as into portions of the southern Appalachians (Rusch et al. 2000). Ruffed grouse are an important game species, particularly in the eastern portion of their range where they are commonly hunted for sport (Kubisiak 1984, Rusch et al. 2000). Normally considered abundant in the northern portion of their range, ruffed grouse populations have experienced long-term declines along the species' southern range margins, including portions of New England (Dessecker and McAuley 2001,

Stauffer et al. 2011, Blomberg et al. 2012). Although habitat loss is generally implicated for population declines, concerns have also been raised about ruffed grouse harvest and timing of harvest as a possible population impact (DeStefano and Rusch 1986, Small et al. 1991, Rusch et al. 2000, Devers et al. 2007, Skrip et al. 2011). As a popular game species, there has been a wide array of research conducted in the eastern portion of the species' range motivated in large part by interest in harvest management and conservation of the species. These studies have evaluated stressors that influence ruffed grouse survival both annually and seasonally, including factors such as brood break-up and juvenile dispersal (Hale and Dorney 1963, Small et al. 1993, Yoder et al. 2004), predator migration (Small et al. 1991), environmental effects associated with seasonal change (i.e. food availability, harsh weather, and protective cover; Svoboda and Gullion 1972, Devers et al. 2007), harvest (e.g. Devers et al. 2007, Skrip et al. 2011), and how variation among individuals may interact with these factors (Larsen and Lahey 1958, Fischer and Keith 1974, DeStefano and Rusch 1986, Small et al. 1991, Devers et al. 2007).

Ruffed grouse hunting seasons vary among and sometimes within states and Canadian provinces. Hunting that extends into winter months is normally considered late-season, and the effects of late-season harvest on ruffed grouse populations has traditionally been of interest to managers and researchers (Kubisiak et al. 1984, DeStefano and Rusch 1986). With the transition into winter, ruffed grouse begin to switch from ground foraging to foraging in trees for buds and catkins (Barber 1961). This transition along with severe weather is thought to increase mortality risk due to greater exposure of budding ruffed grouse to both predators and hunters (Kubisiak et al. 1984). Additional mortality during this transition period through hunting could increase the potential for additive losses to the population (Blomberg 2015), and understanding the timing

and level of harvest with respect to late-season hunting is necessary to improve harvest management.

In the state of Maine, ruffed grouse is a culturally important game species perused by both resident and non-resident hunters, yet there has been little prior research on ruffed grouse demographics in the state, including processes that affect survival and harvest rates. We evaluated weekly survival of radio-marked ruffed grouse at two study areas in central Maine during 2014–2016, to quantify variation in survival, estimate harvest rates, and identify sources of mortality. Our specific objectives were to 1) estimate seasonal and annual variation in survival and harvest, to 2) evaluate sources of temporal, spatial, and individual variation that contributed to differences in survival and harvest, to 3) determine how these sources interact with each other to affect survival, and to 4) examine intra-seasonal variation in harvest to address local concerns over late-season harvest effects on ruffed grouse populations. This is the first study to address survival and harvest rates of ruffed grouse in Maine, provides previously unavailable information to inform management of ruffed grouse in the state, and contributes to the collective range-wide knowledge of the species' ecology and management.

### **Study Area**

We selected two study areas in central Maine, USA, based largely on relevance to ruffed grouse harvest in the state. The first area was comprised primarily of commercially managed forestland, and contained of a mixture of upland forests and wetlands. This area was located in Penobscot and Hancock Counties, along a private forest road commonly referred to as the Stud Mill Road (hereafter Stud Mill; 44°58'N, 68°26'W). Common tree species for this area included balsam fir (*Abies balsamea*), maple (*Acer* spp.), birch (*Betula* spp.), spruce (*Picea* spp.), eastern white pine (*Pinus strobus*), northern white cedar (*Thuja occidentalis*), and big-toothed aspen

(*Populus grandidentata*). The predator community in this area consisted of great horned owl (*Bubo virginianus*), barred owl (*Strix varia*), hawks (*Buteos* spp., *Accipiter* spp.), red fox (*Vulpes vulpes*), fisher (*Martes pennanti*), coyote (*Canis latrans*) and bobcat (*Lynx rufus*). This area was well known to hunters and was open to public access.

The second study area was approximately 2,104 hectares of abandoned farm fields and second-growth upland forests in Waldo County, Maine, the majority of which were located in the Frye Mountain Wildlife Management Area (hereafter Frye Mountain; 44°28'N, 69°13'W). Frye Mountain was owned and managed by the Maine Department of Inland Fisheries and Wildlife. Forest stands at Frye Mountain were comprised of maple, birch, white ash (*Fraxinus americana*), quaking aspen (*Populus tremuloides*), American beech (*Fagus grandifolia*), and balsam fir. This study area was surrounded by a rural landscape comprised of private lands that contained maturing forests and some small-scale agricultural fields. The majority of our work was conducted on the state-owned property, but we also worked on adjacent privately-owned lands as needed based on movements of radio-marked birds. Common predators in this area were similar to those found at Stud Mill Road. Management practices employed at Frye Mountain were designed to promote upland game bird habitat, largely through small-scale clearcutting and field maintenance. This area was also well known as an upland bird hunting destination, and was open to public access. The majority of hunting in both study areas were accomplished by the use of the areas' well-developed road systems.

### **Field Methods**

#### **Trapping**

We captured ruffed grouse during August and September 2014–2016, during October 2015, and during April and May 2015–2016, using traps modified from the lily-pad design described by Gullion (1965). These traps were comprised of 20-m chicken wire fences that

directed ruffed grouse into a wire funnel, which in turn led into a round welded wire trap body with a cloth mesh covering. We checked traps twice each day (late morning and evening) to reduce the frequency of self-inflicted injury by ruffed grouse while in the trap bodies. At initial capture we determined age as adult (>1 year of age) or juvenile (<1 year of age) based on molting stage, and sex based on plumage characteristics (Davis 1969). Captured individuals were weighed using a spring scale ( $\pm 5$  g), and measurements of wing chord, tail, culmen, and tarsus length were taken ( $\pm 0.1$  cm). All birds were fit with an aluminum leg band stamped with a unique identification number, and individuals included in this research were also fit with a 12 g very-high frequency (VHF) radio transmitter (Model A3950; Advanced Telemetry Systems, Isanti, Minnesota), using a necklace-style attachment. Ruffed grouse weighing <375 g at capture did not receive radio transmitters; we chose this weight as a conservative threshold for collaring ruffed grouse because mortality risk may increase when radio transmitters exceed 3% of a bird's body mass (Casas et al. 2015). Transmitters had a maximum battery life of ~18 months and were equipped with a mortality sensor that caused the pulse rate to double after 8 hours without movement. Radio transmitters and leg bands were printed with a toll-free phone number for hunters to report harvested ruffed grouse to the University of Maine Wildlife Demographics Lab.

We monitored radio-marked birds at varying intervals throughout the year to account for changing seasons, study area accessibility, and research objectives related to this and other aspects of our work. During the capture season (August and September) we checked live/dead status of radio-marked individuals daily to detect mortalities that may have been associated with capture and handling. We monitored radio-marked ruffed grouse at least twice weekly during October, and at least once weekly during the latter part of the hunting season (November and December). January through mid-April we monitored ruffed grouse at least once every 2 weeks,

and multiple times each week from May through July. Any time a mortality signal was detected, we recovered the radio-collar and determined the probable cause of death. We classified cause of death as predation, harvest, or unknown, and further classified predation as avian, mammal, or unknown based on field evidence (Bumann and Stauffer 2002, Blomberg et al. 2013). Because we were unable to monitor ruffed grouse with high frequency (e.g. daily) throughout the year, we could not account for confounding factors such as scavenging that may have obscured the true cause of death. As such, our field classifications of cause-specific mortality should be considered conservative and may be biased towards mammalian predators because of the potential for scavenging by mammals to obscure other causes of death. Dead birds that were found fully intact with no obvious signs of trauma were recovered and frozen, and were later examined for evidence of shot using radiographic imaging and necropsy; birds that contained shot were classified as unrecovered crippling loss associated with hunting. At least once each year following the end of the hunting season we used fixed wing aircraft to search for missing birds at each study area, within a distance that approximated the maximum dispersal distance of ruffed grouse (Small and Rusch 1989). Ruffed grouse that survived longer than the maximum battery life of our radio transmitters, or that went missing and could not be located, were presumed to have failed radios and were right-censored from analyses. All capture, handling, and monitoring of ruffed grouse was approved by the University of Maine Institutional Animal Care and Use Committee (protocol number A2014-03-06).

### **Analytical Methods**

#### **Seasonal and Annual Survival**

We estimated weekly survival probabilities for the period 1 October 2014 to 28 February 2017 using nest survival models implemented in Program MARK (White and Burnham 1999) via program R using the package “RMark” (Laake 2013). Nest survival analysis was chosen

because it best-allowed for irregular monitoring of individuals, fitting our study design where frequency of monitoring varied within the year. We constructed a weekly encounter history from our live/dead telemetry data, where week 1 began on October 1<sup>st</sup> during each study year (the beginning of the ruffed grouse hunting season). We analyzed differences in survival based on temporal (year and season), spatial (study area), and individual (age and sex) variables, and included most of these as group covariates in our analysis. We suspected fall, winter, and nesting to be periods of greater mortality for ruffed grouse because they are seasons of increased exposure to predators and periods of harsh conditions. We built models that reflected these hypothesized sources of variation by grouping calendar months into seasonal categories that best-matched the biology of our study system (Fall = Oct–Dec; Winter = Jan–Mar; Spring = Apr–Jun; Summer = Jul–Sep), and we contrasted these seasonal hypotheses with models where survival was allowed to vary independently among months.

We used Akaike's Information Criterion (AICc) to assess model support based on a criteria of 2.0 AICc units (Burnham and Anderson 2002) to contrast models that reflected mutually-exclusive hypotheses (e.g. a seasonal model vs a month model). Variable support was further validated by examining beta coefficients and evaluating whether 95% confidence intervals did not overlap zero. Our model selection was performed using a two-step approach, where we first constructed single-variable models where survival varied only by a single source of variation (i.e., age, sex, study area, year) and compared these to a constant model defined only by the intercept term (Null). Supported variables from the first step were then incorporated into a second step of model selection, where we included hypothesized seasonal structures as both additive and interactive effects with supported variables from the first step (e.g., Season\*Age). We considered full monthly variation during this second step in a similar manner. We converted

weekly survival estimates into monthly survival probabilities as  $S(\text{week})^{4.28}$  (assuming an average of 4.28 weeks in a calendar month), computed annual survival as the product of all monthly survival probabilities, and calculated estimates of variance for monthly and annual survival probabilities using the Delta method (Powell 2007).

We removed individual ruffed grouse from our survival analyses that did not survive a 6-day censoring period following capture. This approach to censoring was justified by an independent analysis, which identified a mortality threshold following capture and release of our radio-marked sample that occurred 6 days following release (Blomberg et al. *in review*). In addition, individuals whose radios failed were recorded as alive based on their last documented radio signal, and were right-censored from the survival history following the last week a signal was obtained.

### **Weekly and Cumulative Harvest**

We estimated weekly and cumulative harvest rates for each hunting season during our study (2014, 2015, and 2016), again using nest survival models implemented in Program MARK (White and Burnham 1999) and RMark (citation). For this analysis we included mortality associated with crippling loss, hunter-reported harvest, and known unreported harvest, such that harvest rates reflect the total mortality associated with harvest and not only that which was reported. We right-censored all individuals that were not harvested but died before the end of the hunting season, by ending their survival histories the week following their death, which allowed us to estimate survival based strictly on hunting-related mortality. In other words, survival estimates in this context reflected the probability that an individual was not harvested, given that it was alive and available to be harvested during a particular week of the season. We constructed models to analyze differences in survival from harvest based on age, sex, study area, and year,

which were included as group variables. We also calculated an individual body condition metric based on a linear regression of tarsus length on mass, and used the residuals of that regression as estimates of size-corrected body mass (Blomberg et al. 2014). We did not consider body condition effects in our larger survival analysis, because we were only able to measure birds once each year, typically before the onset of the hunting season, and therefore our data could not accommodate the presumably dynamic nature of body condition throughout the remainder of the year.

As with our survival analysis, we conducted a two-step model selection process where our first step included basic models of spatial, temporal, and individual variables compared to our null model of constant harvest risk. Supported variables were then implemented into a second, more complex model comparison, where sources of hypothesized intra-annual variation were constructed as both additive and interactive effects. We used criteria for model comparisons and assessment of variable support as defined above. We converted weekly survival probabilities into monthly and annual harvest rates as  $1 - \prod (S_i)$ , and calculated estimates of variance for annual harvest rates using bootstrapping.

## **Results**

We included 248 unique ruffed grouse in our analyses, of which 72 were adult males, 64 were juvenile males, 59 were adult females, and 53 were juvenile females. The majority of these birds (236) were caught during August and September, with a small number (12) captured during the spring. After considering individuals that survived and were available for harvest during multiple years, our sample included 267 grouse/year combinations. Thirty-seven ruffed grouse were harvested and reported by hunters, and we classified an additional 4 deaths as birds shot but

not recovered. We determined that 2 additional birds were harvested but were not reported to us based on field remains (e.g. a collar found hanging from a tree branch with no other remains).

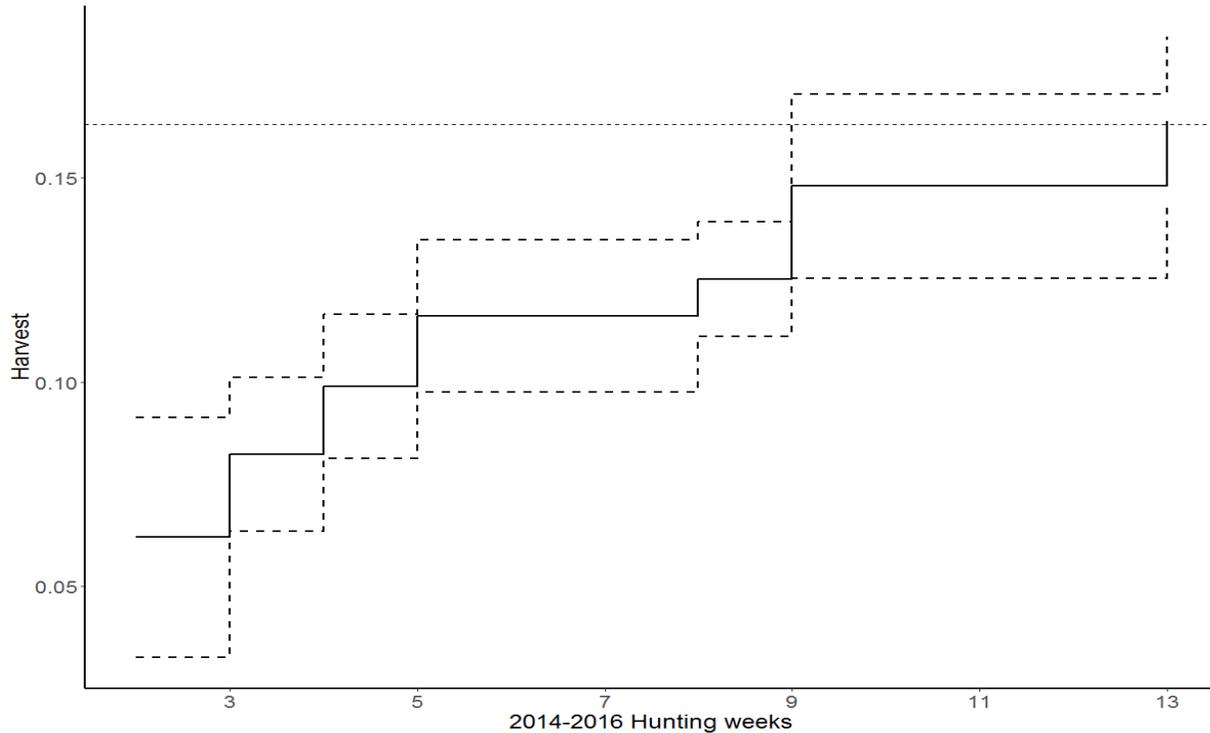


Figure 1.1. Cumulative harvest rates. Weekly cumulative harvest rates of radio-marked ruffed grouse from October through December, 2014-2016, pooled across all years and study area in central Maine USA. The dashed lines represents 95% upper and lower confidence intervals. The cumulative annual harvest rate across three years was indicated by the horizontal dashed line.

Therefore, a total of 43 radio-marked ruffed grouse were shot and killed by hunters over 3 years.

Twenty-six birds were harvested during October, 7 during November, and 10 during December

(Fig. 1.1). An additional 4 radio-marked ruffed grouse went missing during the hunting season

that could have represented additional unreported harvest; however we cannot rule out

alternatives such as radio failure or undetected emigration, and therefore these individuals were

right-censored. We recorded 55 additional mortalities during the hunting season that we

attributed to predation, 20 of which we classified as avian, 17 as mammalian, and 18 where the

predator could not be determined.

Table 1.1. Ruffed grouse mortality. Apparent cause-specific mortalities of radio-marked ruffed grouse, by season, from two study areas in central Maine, 1 October 2014 to 28 February 2017. Harvest mortality occurred only during the fall hunting season, 1 October to 31 December each year.

Season <sup>a</sup>	Predation (% Avian)	Unknown	Harvest <sup>b</sup>	Total Deaths
<b>2014-2015</b>				
Fall	20 (40%)	5	17	32
Winter	21 (62%)	5	-	26
Spring	10 (50%)	2	-	12
Summer	2 (50%)	0	-	2
<b>2015-2016</b>				
Fall	8 (75%)	7	21	36
Winter	12 (33%)	3	-	15
Spring	13 (62%)	2	-	15
Summer	6 (83%)	1	-	7
<b>2016-2017</b>				
Fall	14 (43%)	1	5	20
Winter	4 (50%)	1	-	5

<sup>a</sup> Fall: October-December; Winter: January-March; Spring: April-June; Summer: July-September

<sup>b</sup> Harvest numbers includes birds that were reported, that were presumed unreported, and shot and not recovered.

Forty six mortalities occurred during winter, 37 of which we could confirm as predation (January through March; 19 avian, 10 mammalian, 8 unknown), and 36 mortalities occurred during spring and summer, 31 of which we could confirm as predation (19 avian and 8 mammalian, 4 unknown; Table 1.1). All deaths not confirmed as predation during all seasons reflected cases where the cause of death could not be determined, or where the transmitter could not be recovered.

Table 1.2. Weekly survival model results. Model selection results for weekly survival analysis of radio-marked ruffed grouse at two study areas in central Maine, USA, from 1 October, 2014 to 28 February, 2017. Weekly survival probability was estimated using nest survival analyses in Program MARK. AICc is Akaike’s Information Criterion adjusted for small sample size,  $\Delta$ AICc is the difference in AICc from the top model,  $W_i$  is the model weight, and  $K$  is the number of model parameters.

Models <sup>a</sup>	AICc	$\Delta$ AICc	$W_i^b$	$K^c$
Month + Age	1452.34	0	0.91	13
Spring/Summer + Age	1458.43	6.10	0.04	4
Seasons + Age	1459.50	7.16	0.03	5
Month	1460.64	8.30	0.01	12
Fall/Winter + Age	1464.56	12.22	0.00	4
Month * Age	1464.79	12.45	0.00	24
Seasons * Age	1464.87	12.53	0.00	8
Spring/Summer * Age	1465.76	13.43	0.00	6
Fall + Age	1466.03	13.70	0.00	3
Fall * Age	1467.43	15.09	0.00	4
Spring/Summer	1467.71	15.40	0.00	3
Fall/Winter * Age	1467.94	15.60	0.00	6
Seasons	1468.49	16.15	0.00	4
Age	1470.74	18.40	0.00	2
Age + Sex	1472.48	20.14	0.00	4
Fall/Winter	1473.21	20.89	0.00	3
Fall	1474.93	22.63	0.00	2
Age * Sex	1476.20	23.86	0.00	6
Null	1481.02	28.68	0.00	1
Sex	1482.25	29.91	0.00	3
Site	1482.30	29.95	0.00	2
year	1484.97	32.63	0.00	3

<sup>a</sup> Month: Calendar Month; Spring/Summer: fall and winter months grouped together (Oct-Mar) and spring (Apr-Jun) and summer (Jul-Sep) months are independent of each other; Season: 4 Seasons (fall = Oct-Dec, winter= Jan-Mar, spring= Apr-Jun, and summer= Jul-Sep) separated into a weekly time scale; Fall/Winter: fall and winter months separated into a weekly time scale and spring and summer months are grouped together; Fall: fall months compared to the rest of the year in a weekly time scale; Age: Adult (>1 year) vs. juvenile (<1 year); Sex: Male vs. female; Year: full weekly survival for fall 2014 through 2015 and fall 2015 through 2016; Null: survival constant (intercept -only).

Our best performing model of weekly survival included a monthly time structure with an additive effect of age (Table 1.2), which indicated juvenile ruffed grouse had a lower probability of survival than adults ( $\beta = -0.49 \pm 0.15$  SE; Fig. 1.2B).

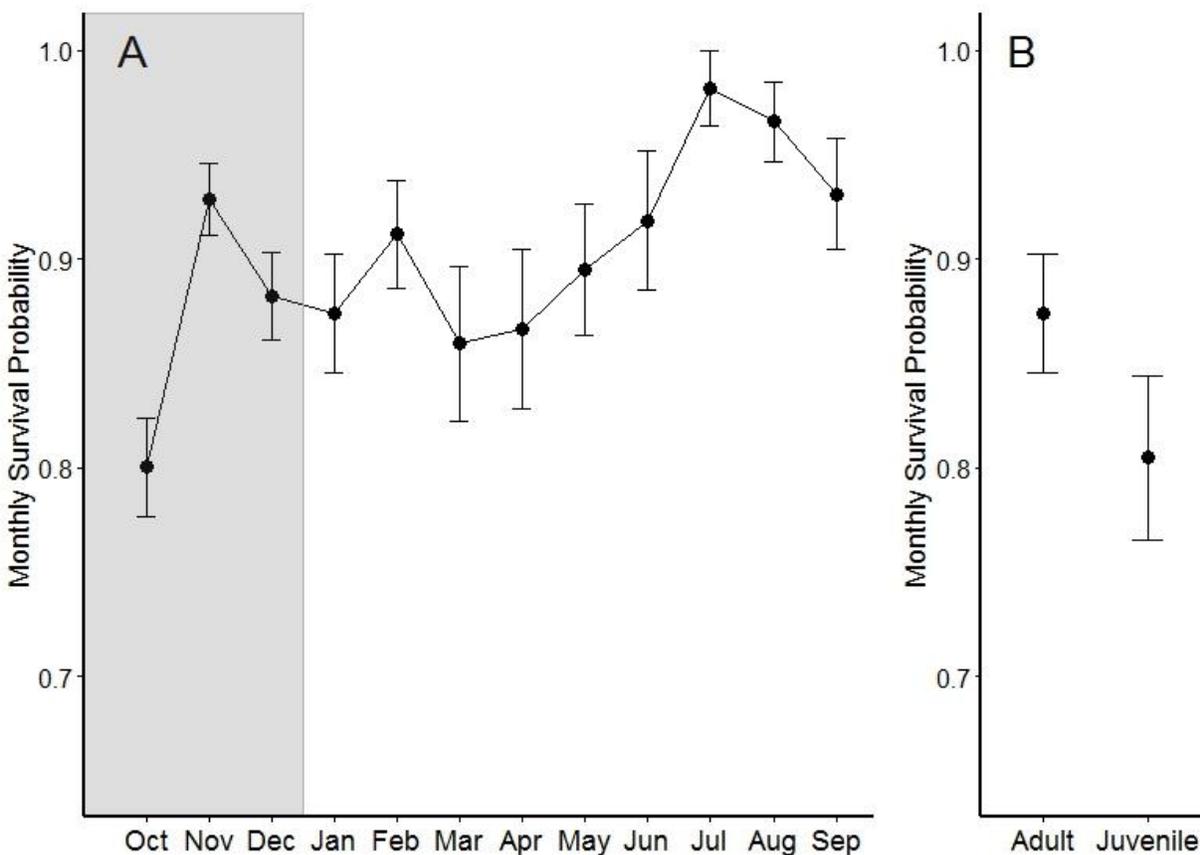


Figure 1.2. Ruffed grouse monthly survival throughout the year. A) Monthly survival probabilities of adult (>1 year of age) radio-marked ruffed grouse, by month, during 2014–2016 in central Maine, USA. B) Monthly survival estimates illustrating the age-specific difference in survival between adult and juvenile (<1 year of age) ruffed grouse. Estimates were derived from the most competitive model, where survival varied by month with an additive age effect. For B) we used January as a reference month to illustrate age-specific differences. The shaded gray box represents the hunting season in Maine (October–December). Error bars reflect standard error (SE).

The monthly time structure indicated both age classes had the lowest survival probability during October and highest survival probability during July (Fig 1.2A; Table 1.3). The mean annual survival probabilities during our 3-year study for adults and juveniles were  $0.28 (\pm 0.01 \text{ SE})$  and  $0.13 (\pm 0.003 \text{ SE})$ , respectively. We did not find support for effects of sex, study area, or year on survival (Table 1.2).

Table 1.3. Monthly survival probabilities of ruffed grouse. Monthly survival probabilities of radio-marked adult and juvenile ruffed grouse in central Maine, USA during 2014–2016 at two study areas.

Month	Survival <u>Adult</u> <sup>a</sup>	SE (Adult)	Survival <u>Juvenile</u> <sup>a</sup>	SE (Juvenile)
Oct	0.800	0.024	0.700	0.028
Nov	0.929	0.017	0.887	0.026
Dec	0.882	0.021	0.817	0.029
Jan	0.874	0.029	0.805	0.040
Feb	0.912	0.026	0.861	0.038
Mar	0.859	0.037	0.784	0.051
Apr	0.866	0.038	0.794	0.053
May	0.895	0.031	0.836	0.045
Jun	0.918	0.033	0.871	0.049
Jul	0.982	0.018	0.970	0.029
Aug	0.966	0.019	0.945	0.030
Sep	0.931	0.026	0.891	0.039

<sup>a</sup> Adult > 1 year of age; Juvenile < 1 year of age

Our top performing harvest models allowed survival to vary by week, with an additive effect of study area and age (Table 1.4). Survival was greater (i.e. lower likelihood of harvest) at Stud Mill than at Frye Mountain ( $\beta=0.72 \pm 0.38$  SE) indicating higher harvesting rates at Frye Mountain (Fig. 1.3A). For both Frye Mountain and Stud Mill, harvest rates became progressively smaller as the season progressed (Fig. 1.2), with greater cumulative harvest during October (Frye Mountain  $H_{Oct}= 0.14 \pm 0.02$  SE; Stud Mill  $H_{Oct} = 0.07 \pm 0.02$  SE) that was double that of the total harvest that occurred during November and December (Frye Mountain  $H_{Nov-Dec}= 0.07 \pm 0.02$  SE; Stud Mill  $H_{Nov-Dec}=0.03 \pm 0.01$  SE). Although age was included in the best-supported model, further evaluation of the beta coefficient and confidence intervals showed a lack of support, with 95% confidence intervals overlapping zero. When all sources of harvest were accounted for (reported harvests, crippling losses, and unreported harvests), the cumulative

harvest rates during 2014, 2015, and 2016 were  $0.172 \pm 0.01$ ,  $0.194 \pm 0.01$ , and  $0.077 \pm 0.01$ , respectively, and the mean probability of an individual ruffed grouse being harvested during our

Table 1.4. Weekly harvest model results. Weekly harvest analysis of radio-marked ruffed grouse at two study areas in central Maine, USA, from 1 October, 2014 to 31 December, 2017. AICc is Akaike's Information Criterion adjusted for small sample size,  $\Delta$ AICc is the difference in AICc from the top model,  $W_i$  is the model weight, and  $K$  is the number of model parameters.

<u>Models<sup>a</sup></u>	AICc	$\Delta$ AICc	$W_i$	$K$
Week + Site + Age	369.19	0.00	0.53	15
Week + Site	370.81	1.62	0.24	14
Week + Age	372.09	2.90	0.12	14
Week	372.42	3.23	0.11	13
Week * Site	384.51	15.32	0.00	26
Month + Site + Age	387.99	18.81	0.00	5
Week * Age	388.76	19.58	0.00	26
Month + Site	389.59	20.40	0.00	4
Month + Age	390.88	21.70	0.00	4
Month	391.20	22.01	0.00	3
Time trend + Site + Age	392.10	22.91	0.00	4
Month * Site	392.62	23.43	0.00	6
Time trend + Site	393.73	24.54	0.00	3
Time trend * Site	393.78	24.60	0.00	4
Month * Age	394.74	25.55	0.00	6
Time trend + Age	394.95	25.76	0.00	3
Time trend	395.29	26.10	0.00	2
Quadratic + Site	395.37	26.19	0.00	4
Quadratic + Age	396.58	27.39	0.00	4
Quadratic	396.94	27.75	0.00	3
Time trend * Age	396.95	27.76	0.00	4
Age + Site	398.55	29.36	0.00	3
Age * Site	399.52	30.33	0.00	4
Site	400.60	31.41	0.00	2
Age	401.69	32.50	0.00	2
Null	402.26	33.08	0.00	1
Year	403.21	34.03	0.00	3
Body Condition	404.26	35.07	0.00	2
Sex	404.93	35.74	0.00	3

<sup>a</sup> Month: Calendar Month during hunting season (October-December); Site: Frye Mountain vs. Stud Mill; Age: Adult (>1 year) vs. juvenile (<1 year); Sex: Male vs. female; Year: full weekly survival for individual hunting seasons of 2014, 2015, and 2016; Null: survival constant (intercept -only).

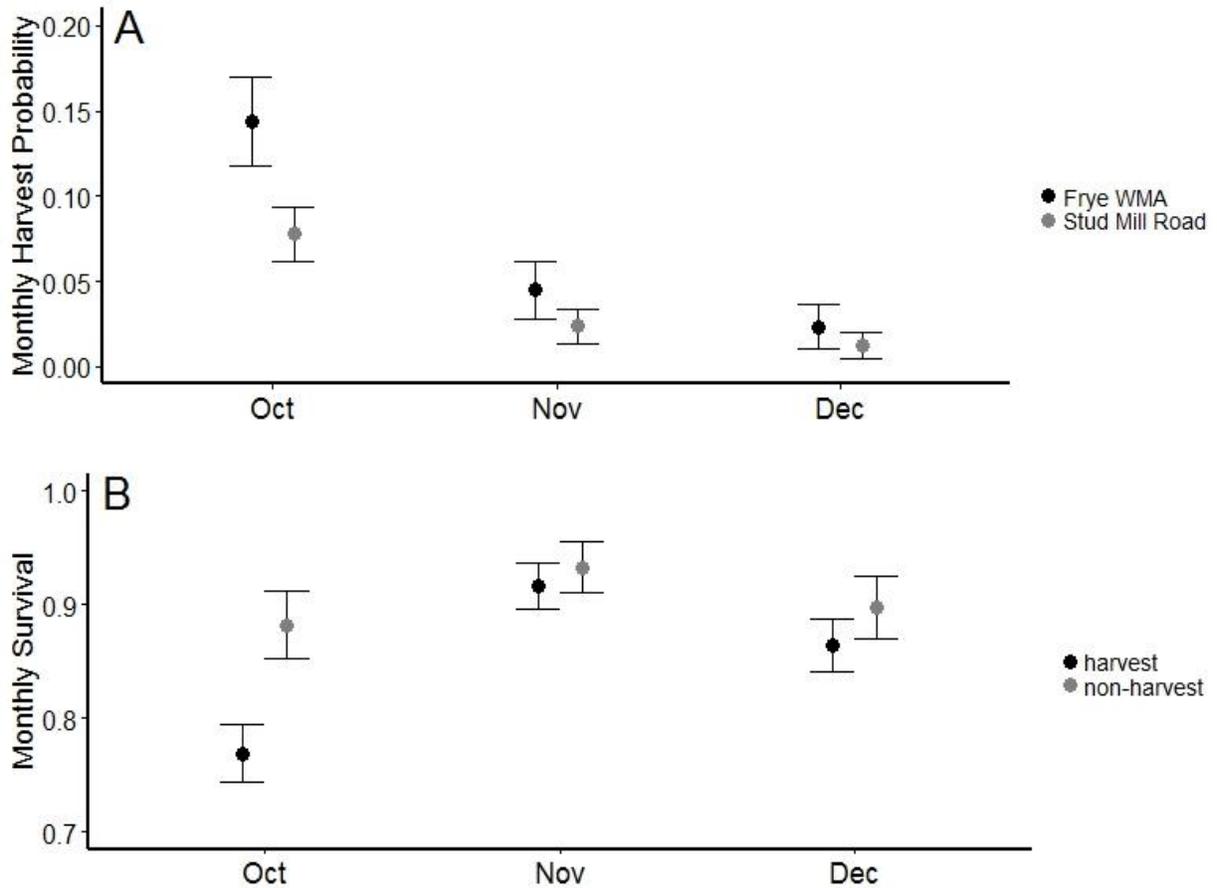


Figure 1.3. Survival and harvest of ruffed grouse A) Monthly harvest probabilities of radio-marked ruffed grouse between two study areas in central Maine, USA. Estimates were derived from the most competitive model, where study area was an additive effect. B) Monthly survival probabilities of radio-marked ruffed grouse during the hunting season when harvest is included (harvest) and the monthly survival probability associated with only non-harvest mortality (non-harvest); the difference between these two values reflects the monthly harvest rate, pooled across all years. Error bars reflect standard error (SE).

study was 0.16 (95% CI = 0.14-0.18; Fig. 1.2). Our results suggested that October harvest was a large contributor to the more general reduction in survival during that month, accounting for approximately half of the mortality that occurred in October (Fig. 1.3B). We did not find support for differences in harvest between sexes, among years, or based on individual body condition at time of capture (Table 1.4).

## Discussion

We found individual variation in monthly survival was related to age and differences in harvest rates between study areas, and we found that ruffed grouse experienced higher survival during the summer months and lower survival during the fall and winter months. The temporal patterns in survival we observed were partially attributed to hunting. Survival during October was lower than any other month throughout the year, due primarily to reductions in survival through harvest. If mortality related to harvest was discounted from October survival, the lowest period of seasonal survival was associated with winter months, followed by fall, spring, and summer. This result illustrates that harvest was the primary cause of reduced survival during October, but not during the latter portions of the hunting season. The large proportional effect of harvest in October may also explain why a model allowing full monthly variation in survival was better-supported than one that condensed survival into biologically-meaningful seasons. Other studies of ruffed grouse have quantified harvest rates in addition to other sources of mortality, and typically fall and winter are reported as having lower survival than spring and summer (Bump et al. 1947, Rusch and Keith 1971, Thompson and Fritzell 1989, Small et al. 1991, Devers et al. 2007, Skrip et al. 2011), similar to our results.

In addition to increased mortality due to harvest, other factors, such as raptor migration, phenological changes, and weather, may have contributed to the seasonal patterns in survival we observed. We found that the majority of predation on ruffed grouse in Maine was attributed to avian predators, which were likely a combination of migratory and resident raptors, depending on the time of year. Avian predation appears to be the primary source of mortality for ruffed grouse, but it is unclear how much of this predation is associated with raptor migration or resident avian predators (Rusch and Keith 1971, Small et al. 1991, Devers et al. 2007). In

western Utah, a study of seasonal survival of chukar (*Alectoris chukar*) found that survival during the fall was reduced during the peak of raptor migration (Robinson et al. 2009); however a similar study of greater sage-grouse (*Centrocercus urophasianus*) in nearby Nevada showed no correlation between fall survival and raptor migration (Blomberg et al. 2013). As a non-migratory gamebird, ruffed grouse must tolerate harsh weather, loss of protective cover due to vegetative senescence, and use of alternate food sources, all coincident with the onset of winter (Gullion 1966, Thompson and Fritzell 1988). Despite having adapted to these conditions, ruffed grouse are usually documented as having high fall and winter mortality. Risk of mortality is most likely increased during this time due to less concealment when foraging as well as inadequate thermal protection during periods of harsh weather conditions (Larsen and Lahey 1958, Kubisiak et al. 1984), particularly when snow cover is insufficient for snow roosting (Thompson and Fritzell 1988).

Annual survival rates during our study were similar to those reported in other studies of ruffed grouse, particularly those in the northern portion of their range. In Wisconsin, Small et al. (1991) reported an annual survival of 25% for adults and 7% for juveniles. Annual survival rates in Alberta were 27-30% (Rusch and Keith 1971), and Gutierrez et al. (2003) reported 11% annual survival for ruffed grouse in Minnesota. In general annual survival rates were slightly higher in the southern portion of ruffed grouse range than what we reported for Maine. During the early 20<sup>th</sup> century in New York, annual survival of ruffed grouse was reported at 42% to 50% (Bump et al. 1947), and more recently Skrip et al. (2011) quantified survival over a 6-month period and reported rates of 38% and 52% for two study areas. In the Appalachian region across 12 study areas and 8 states, Devers et al. (2007) reported annual survival that ranged from 17%–

57% among sites and years, where the lowest survival was in a study area located in Ohio and the highest was in an area in West Virginia.

Adult ruffed grouse had higher survival during our study than juveniles. The difference in age-specific survival could be a result of different stressors experienced during each life phase. Ruffed grouse undergo a fall natal dispersal period where juveniles break away from broods in search of new territories (Godfrey and Marshall 1969, Small and Rusch 1989, Hannon and Martin 2006). Natal dispersal is thought to negatively affect juvenile survival, because it increases movement requires individuals to move through unfamiliar areas, and in the case of fall dispersal overlaps with hunting, raptor migration, and the seasonal environmental changes previously mentioned (Small et al. 1993, Yoder et al. 2004, Hannon and Martin 2006). Small et al. (1993) evaluated ruffed grouse movements associated with fall and spring dispersal for both juveniles and adults, and found that juveniles had lower survival than adults during both transient and colonization phases of dispersal. Similarly, Yoder et al. (2004) found that juvenile ruffed grouse moving into unfamiliar areas had an increased risk of mortality during dispersal. Ruffed grouse in Alberta and Wisconsin exhibited similar differences in survival by age, where adults had higher survival than juveniles (Fischer and Keith 1974, Small et al. 1991). However, in the Appalachian region and in Minnesota, ruffed grouse survival was not found to differ among age classes (Gutierrez et al. 2003, Devers et al. 2007). Age-specific survival has been evaluated in many gamebird species, with a general consensus of greater survival in adults than juveniles (Lindström 1994, Hannon and Martin 2006, Rolland et al. 2010, Pekkola et al. 2014).

When data were pooled across years and between study areas, we estimated a 16% harvest rate for Maine ruffed grouse. This estimate was derived from two study areas over 3 years, and we believe it to be generally reflective of harvest experienced in the more popular

hunting areas for ruffed grouse in the state, however our study areas may have experienced greater rates of harvest than other portions of the state that were less well known or not publicly accessible. The level of harvest we observed is comparable to some, but not all, previous studies of ruffed grouse, and generally our results fall in the middle of reported harvest rates. In New York, harvest rates were reported at 13-20% in the early 20<sup>th</sup> Century (Bump et al. 1947), and more recently Skrip et al. (2011) reported that 11% of radio-marked ruffed grouse were harvested. In Wisconsin, DeStefano and Rusch (1986) reported a mean harvest rate of 40% during a 4-year period, while Small et al. (1991) reported a mean harvest rate of 28% during a 6-year study. In Alberta, harvest rates for ruffed grouse were reported at 19-48% (Fischer and Keith 1974). During an extensive study in the Appalachian region, harvest was characterized for 7 study areas with a reported range of 6%-37% harvest rates, with rates varying both among study sites and among years within study sites (Devers et al. 2007).

We found that shot but unrecovered birds and unreported harvest were relatively infrequent when compared to reported harvest. Among ruffed grouse whose deaths we attributed to harvest, we classified 9% as shot but unrecovered, and an additional 5% were confirmed as harvested but unreported. Similar rates of crippling loss have been documented among ruffed grouse and other gamebird species. In northern Wisconsin, DeStefano and Rusch (1986) documented a mean crippling loss of 13% during a 3 year study obtained through field questionnaires completed by hunters, and in willow ptarmigan (*Lagopus lagopus*) Sandercock et al. (2011) reported a 7% unrecovered rate during a 3-year study. The levels of unrecovered harvest we observed reflects 9% of the total harvest mortality or approximately 1.4 % of birds available to be harvested during the hunting season, and as such unrecovered birds appear to have minimal effects on the overall impacts of harvest on survival. However, the rate of

unrecovered loss we observed should be viewed as a conservative estimate of the total effect of crippling on marked birds, because we could not account for confounding factors such as predation on crippled individuals or savaging that may have occurred before we were able to detect a shot but unrecovered bird.

We observed a difference in harvest between study areas, where the study area centered on the State Wildlife Management Area (Frye Mountain) experienced higher rates of harvest than the study area comprised of private commercial forest (Stud Mill). Both study areas were open to unrestricted public access during the hunting season, and were well-known areas within the region for small game hunting. Because hunters reported their harvests directly to us, we documented the number of birds harvested by each individual hunter each season. At Frye Mountain, one local hunter was responsible for 45% of the total harvest, and clearly this individual's high success was a primary driver of differences between the two study areas. However, we do not believe this reflects an inherent bias in harvest rates, because variability in success among individual hunters is likely a common factor affecting harvest in general. Individual hunter effort has been evaluated in other taxa, and hunter experience and skill level consistently result in higher harvest success for certain individuals. For example, furbearer trapper effort and skill are important determinants of individual trapper success, particularly when targeting certain species that proved to be more difficult to harvest than others, and this results in substantial heterogeneity in success among individual trappers (Banci and Proulx 1999). In recreational fisheries, anglers that had more experience and a higher skill level were more likely to produce density-dependent catchability, meaning that more-skilled anglers were more likely to obtain high catches when stock density was low compared to less-skilled anglers (Ward et al. 2013). While our observed difference in harvest rates between study areas was likely

caused by heterogeneity in individual hunter success, we suggest this effect may be fairly ubiquitous for ruffed grouse harvest in general.

Temporal variation in the timing of harvest is an important consideration when managing harvested species. Our study was driven, in part, over local concerns about the length of ruffed grouse hunting seasons, particularly when late-season hunting coincided with the transition of birds from ground foraging to budding in trees during winter. This transition is thought to both increase vulnerability, and also lead to greater mortality of individuals otherwise likely to survive until the next breeding season (Kubisiak et al. 1984). Our results illustrated that harvesting occurred at greater rates early in the season (October) and were lower during the latter 2 months (November and December). Similar harvest patterns were observed in Wisconsin and New York, where monthly hunting mortality decreased from the start of the hunting season to later in the season (DeStefano and Rusch 1986, Small et al. 1991, Skrip et al. 2011). Alternatively, in the Appalachian region, Devers et al. (2007) reported high harvest at the beginning of the hunting season (October and November), lower harvest in the middle of the season (December) and an increase in harvest at the end of the season (January and February), demonstrating the potential for harvest rates to increase with an increase in hunting season length. In Maine, lower harvest during November and December may result from hunters shifting their focus to alternative species (e.g. white-tailed deer; *Odocoileus virginianus*) whose hunting seasons begin later in the fall. The seasonal transition to winter may have also limited hunter access to desired areas and lowered harvest rates during the latter portion of the season.

Our study design was observational, rather than experimental, and so we cannot directly evaluate evidence for additive versus compensatory effects of harvest mortality on ruffed grouse survival in Maine. A number of studies conducted such experiments on game bird populations,

including ruffed grouse. Devers et al. (2007) conducted a before-after experimental design of closed and open hunting areas for ruffed grouse in the Appalachian region to disentangle the effects of hunting on survival in those areas. They reported a mean harvest rate of 8% on controlled areas (areas open to hunting during the study) and a mean harvest rate of 20% for treatment areas (areas closed to hunting half way through the study) prior to closure. In the absence of hunting on treatment areas, ruffed grouse survival did not increase compared to areas that were open to hunting, suggesting that harvest mortality was compensatory at the level of harvest reported (Devers et al. 2007). One study in Wisconsin found differences in harvesting rates between private and public lands that illustrated spatial variability in additive versus compensatory mortality for ruffed grouse. Harvest rates on public lands were reported at 48% versus 10% for private lands, suggesting additive mortality effects on the more heavily hunted public lands (Small et al. 1991). In willow ptarmigan, Sandercock et al. (2011) evaluated 3 different rates of harvests (0%, 15%, and 30%) that were randomly assigned to designated study areas, and found that 15% harvest rates were partially compensatory, whereas 30% harvest was additive to non-harvest mortality. Although we cannot conclusively evaluate evidence for additive versus compensatory mortality in our study system, some of our results do provide suggestive insights. We observed differences in harvest rates between study areas, with Frye Mountain having nearly twice the harvest rate as Stud Mill. However we did not find any evidence to support a similar difference in overall survival between study areas, which is consistent with (although not conclusive of) the higher harvest at Frye Mountain being compensated by reduced mortality following harvest. Accordingly, we found that most harvest mortality occurred early in the season, and substantial non-harvest mortality occurred over-winter. This suggests that there is at least high potential for compensation to occur within this

system if over-winter mortality is affected by density-dependent processes (Ellison 1991, Blomberg 2015). Finally, the harvest rates we observed fall within the range of values that have previously been reported as compensatory for ruffed grouse (Bump et al. 1947, Small et al. 1991, Devers et al. 2007). Collectively these results suggests at least a high (albeit not conclusive) likelihood that harvest mortality was partially or fully compensatory in this system.

### **Management Implications**

Our study has addressed a lack of information of ruffed grouse population demographics in Maine and will allow for better-informed harvest regulations moving forward. Patterns in survival of Maine ruffed grouse appear to be similar to other populations, specifically within the eastern portion of their range. Our results indicate that harvest is not excessive during the late-season, and current hunting regulations produced overall rates of harvest that fell well within the range of values reported in other studies. As such, we recommend hunting regulations remain at current levels, and that additional monitoring should be used to evaluate population responses to any changes in harvest rates that occur in the future. We recommend that future ruffed grouse studies in Maine focus on additional study areas throughout the state that may experience different levels of hunting pressure or different levels of environmental variation.

## CHAPTER 2

# SELECTION OF DRUMMING LOCATIONS BY MALE RUFFED GROUSE AND EFFECTS ON DRUMMING BEHAVIOR IN CENTRAL MAINE, USA

### Abstract

Resource selection reflects behavioral choices that species make within their environment, but the fitness consequence of these choices are not always well understood. Ruffed grouse (*Bonasa umbellus*) are popular game birds that are widely distributed across the northern United States and Canada. Ruffed grouse are forest-reliant species that are primarily associated with early successional forest, where males establish and defend territories year round. We evaluated structural habitat selection at breeding display sites and the effects on breeding behavior of male ruffed grouse in central Maine, U.S.A during April and May 2015–2016. We used resource selection functions (RSFs) to compare habitat characteristics at used display locations with those at available locations, and we further assessed how selected habitat features from the RSFs were associated with three ruffed grouse display (drumming) characteristics: drumming rate per hour and wing beat rate per drum. We found that male ruffed grouse selected drumming locations with high total stem density, as well as high conifer stem density within 5m from the display stage. However we did not find that these same variables were associated with drumming behaviors, suggesting no effect of habitat selection on breeding display behavior. This study was a step towards understanding the possible consequences of male habitat selection on mating displays.

## Introduction

An animal's primary goal is to increase its fitness through survival and reproductive success, which is accomplished, in part, by acquiring resources to devote towards reproduction and self-maintenance (Mayor et al. 2009). Resource selection is described by Johnson (1980) as the disproportional use of a resource. Habitat studies based on principles of resource selection (Johnson 1980, Boyce et al. 2002) are often used in conservation and management, where evidence for selection of resources provides information on important habitat components that presumably benefit individual fitness and population growth (Manly et al. 1989, Boyce et al. 2002). Using resource selection studies to inform management is particularly beneficial for species that are often associated with human land use practices, such as timber harvesting, where information on resource selection can guide land use practices to either minimize impacts or produce net benefits to the species (Zimmerman et al. 2007). Despite the importance of understanding habitat selection for management, there have been relatively few studies that evaluate the consequences of selection to components of animal fitness (e.g. Aldridge and Boyce 2007, Mayor et al. 2009, Gibson et al. 2016). This may be particularly true for popular game species, which often have long-standing research on habitat relationships, but may lack a full understanding of the species ecology that is associated with selected habitat features.

Ruffed grouse (*Bonasa umbellus*) are popular game birds that are distributed across the northern United States and Canada, where they are primarily associated with early successional forests (Rusch et al. 2000). Males establish and defend territories of ~300m radius, and select elevated structures that are typically, but not limited to, fallen logs. These elevated structures serve as display stages where males perform to attract females during the spring breeding season (Bump et al. 1947, Gullion 1967, Archibald 1976, Kubisiak 1989). Male ruffed grouse perform

an acoustic display that is produced by rapidly beating their wings, creating a low frequency drum (Rusch et al. 2000, Zimmerman et al. 2007). In addition to attracting females, these audible displays may also attract predators, and when selecting a display stage males must balance resources that will promote their own survival while also fostering reproductive success (Bergerud and Gratson 1988). Because of the unique nature of these displays, a large number of studies have documented characteristics of display stages and the habitat around them (Bump et al. 1947, Palmer 1963, Gullion 1967, Boag and Sumanik 1969, Thompson and Fritzell 1989b, Zimmerman et al. 2007, Zimmerman and Gutiérrez 2008, Berkeley and Gutierrez 2017). In general, ruffed grouse display sites are characterized by high amounts of cover, normally comprised of high woody stem density or dense shrub cover at some distance away from the stage, as well as open visibility around the stage (e.g. within 1 m) for display purposes (Palmer 1963, Boag and Sumanik 1969, Zimmerman et al. 2007, Hansen et al. 2011).

In addition to the importance of habitat structure, studies have also evaluated the role of forest composition as a habitat characteristic for ruffed grouse. One prevailing hypothesis is that cover provided by conifers is inferior to that of deciduous trees, and that when given the choice males will select deciduous stands (Boag 1976, Zimmerman and Gutiérrez 2008, Berkeley and Gutierrez 2017). Stoll et al. (1979) reported that perennial display stages (those used across multiple years) had fewer conifer trees than transient stages (those used only once), suggesting general avoidance by conifer stems by displaying males. Similarly Boag and Sumanik (1969) reported that display stages were in canopy cover primarily dominated by deciduous trees. Conversely, in New York, Bump et al. (1947) reported that display stages were associated with conifers when possible, while Hansen et al. (2011) found no preference for woody species composition at display stages in South Dakota. A more recent study in Minnesota evaluated

breeding displays of male ruffed grouse between stands dominated by either deciduous trees (aspen; *Populus* spp.) or stands dominated by conifer trees, which are used less frequently. The authors predicted that males in conifer stands would display more often to attract females to these presumably suboptimal stands, however, they found no difference in drumming displays between the two cover types, suggesting that use of conifer stands did alter male ruffed grouse behavior relative to deciduous stands (Berkeley and Gutierrez 2017). Thus the role of conifers in ruffed grouse habitat ecology in general, and for male breeding behavior specifically, remains equivocal.

We studied the habitat ecology of male ruffed grouse at two study areas in central Maine, U.S.A during the breeding season (early April through May) 2015–2016. Our objectives were to evaluate third-order habitat selection (Johnson 1980) of male ruffed grouse, and to determine how habitat characteristics selected by males at display stages affect display behavior during the breeding season. In doing so we evaluated both structural habitat characteristics around display sites, and also evaluated specifically whether conifer composition surrounding display stages was related to resource selection. We used acoustic recording devices to measure ruffed grouse breeding display traits, and related display characteristics of individual males to habitat characteristics selected for display stages. We predicted that males would select display locations with little visual obstruction around the stage but with greater stem density in the surrounding area. We further expected that males would display more frequently when using locations with greater values for selected habitat characteristics because an individual may feel more secure, have access to better resources, or be in higher body condition reducing possible restriction on drumming displays.

## Methods

### **Study Area**

We located ruffed grouse display stages in two study areas in central Maine, U.S.A. The first was an area of commercially-owned forested land, comprised of a mixture of wetlands and upland forest, located in Penobscot and Hancock Counties (44<sup>o</sup>58'N, 68<sup>o</sup>26'W). This area is locally referred to as Stud Mill Road. The forest composition in this area was a mix of conifer and deciduous trees with generally high densities of conifers throughout the area. Common tree species included balsam fir (*Abies balsamea*), maple (*Acer* spp.), birch (*Betula* spp.), spruce (*Picea* spp.), eastern white pine (*Pinus strobus*), northern white cedar (*Thuja occidentalis*), and big-toothed aspen (*Populus grandidentata*). Our second study area was located at the Frye Mountain Wildlife Management Area (Frye Mountain), which contained approximately 5,200 acres of second-growth upland forests located in Waldo County (44<sup>o</sup>28'N, 69<sup>o</sup>13'W). Forest composition was a mix of conifer and deciduous trees but with a typically greater density of deciduous trees compared to Stud Mill Road. Common tree species for this area consisted of maple, birch, white ash (*Fraxinus americana*), quaking aspen (*Populus tremuloides*), American beech (*Fagus grandifolia*), and balsam fir. Additional descriptions of the study areas can be found in chapter 1.

### **Display Locations**

During April and May, 2015 – 2016, we located ruffed grouse at display stages during the first 4 hours after sunrise. We located some stages using radio-marked individuals that were captured and marked as part of a concurrent study of ruffed grouse survival and harvest as described in chapter 1, and we supplemented our sample by locating stages of unmarked drumming males that we detected while searching for radio-marked birds or while conducting other field work. Once display stages were located, we used handheld GPS units to record the

stage coordinates, and classified each as a primary ( $\geq 20$  droppings) or a secondary ( $< 20$  droppings) stage based on revised classification from Gullion (1967) and Hansen et al. (2011). We then deployed an automated acoustic recorder (Model 2: SongMeter, Wildlife Acoustics Inc., Maynard, MA, USA), which we set  $\sim 1$  meter from the stage, concealed with locally-available debris. The recorder microphones were positioned perpendicular to the presumed orientation of the male while on the display stage, which we established based on the location of droppings (Garcia et al. 2012a). We deployed recorders at each display stage for 3 days, but left the unit out for one additional day when there was substantial precipitation that might have potentially impacted drumming. Recorders were set to record continuously for 4 hours each morning beginning 30 minutes before sunrise. All monitoring of ruffed grouse for this work was approved by the University of Maine Institutional Animal Care and Use Committee (protocol number A2014-03-06).

### **Vegetation Sampling**

During May and early June we measured vegetation characteristics at each drumming stage and at 2 locations placed at a random direction and distance (50-200m) from the stage, which approximated the typical area of a male home range during the spring breeding season ( $\leq 200$ m; Palmer 1963, Thompson and Fritzell 1989, Hansen et al. 2011). Random locations were placed at least 50 m from the stage to achieve some degree of independence between the used and random locations (Lovallo et al. 2000). The upper distance of 200m was consistent with the estimates of Kubisiak (1989) for proximity between neighboring male ruffed grouse during high density years in Wisconsin, and also approximates upper distance thresholds that have been used to explore ecologically-similar scales in other studies of drumming male ruffed grouse (Zimmerman et al. 2007). The first random point was projected using a randomly chosen

compass azimuth and the second point used an azimuth perpendicular to the first to prevent random locations from occurring adjacent to each other. If a random point fell in a non-forested area the point was moved to the nearest forest edge, which we defined as a location characterized by canopy cover of tree species having woody stems taller than breast height. At display locations, plot centers for vegetation sampling were defined by the display stage, whereas at random locations we centered plots on the closest object to the projected location that could function as a display stage, typically a log (>10cm diameter and elevated; (Hansen et al. 2011). At all used and random locations we sampled tree basal area, visual obstruction, and woody stem density to assess local site vegetation structure and composition. We measured basal area ( $\text{m}^2/\text{ha}$ ) using a 10-factor wedge prism, and we recorded trees by species and further aggregated species into conifer vs deciduous categories. Percent visual obstruction was measured using a 25cm by 25cm board, painted in a checkered pattern of 5cm by 5cm squares, which we modified from Nudds (1977). Cover boards were placed at plot center (i.e. on the display stage or plausible stage), and observers recorded the number of squares  $\geq 50\%$  visible at a 3m distance and 1m height. We repeated these measurements in each of the cardinal directions, and averaged across readings to obtain the mean visual obstruction of each stage. We used a 30m belt transect, which we oriented perpendicular to used and available display stages, and counted all woody stems <10cm dbh within 1m of the transect line. We aggregated stem counts by species class (i.e., deciduous, conifer, or exotics) and also recorded counts based on distance bins that were located 5m, 10m, and 15m from the plot center. We converted counts of stems into stem density (stems/ha) within each distance class.

## Analytical Methods

### **Display Stage Selection**

We evaluated habitat selection using resource selection functions (RSFs; Boyce et al. 2002) in a use versus available design. Generalized linear models were constructed in Program R (R Core Team 2013) to reflect hypotheses about male selection of habitat characteristics at display locations using measured vegetation characteristics as predictive covariates. We aggregated stem density into total stems per hectare within each plot, and further quantified the densities of stems within 5-, 10-, and 15-m (total) from the display stage. This allowed us to evaluate not only the role of stem density in male display site selection, but also whether there were subtle differences in the scale at which males related to protective cover surrounding their drumming stages. We also considered stem density measures separately for deciduous, conifer, and exotic stem classes, in addition to all stems. Similarly, we grouped basal area into deciduous, conifer, and combined basal area classes. Thus, we focus this analysis on how both structural (i.e. stem density, basal area, horizontal cover) and compositional (i.e. conifer vs deciduous basal area and stem density) traits affect habitat selection by male ruffed grouse. Prior to constructing our models, we Z-standardized all covariates and evaluated all pairwise correlations among variables, where those with a Pearson correlation  $>0.60$  were considered highly correlated and were not considered in the same model. We also conducted a preliminary analysis to evaluate differences in habitat variables between primary and secondary display stages. This showed no support for differences in habitat covariates between the two stage classes, so we pooled data for the resource selection analysis. We compared a series of single covariate models to an intercept-only null model, where we considered individual variables supported when they were better-supported by the null based on AICc scores (Burnham and Anderson 2002), and we further

validated covariate support by interpreting slope coefficients from the best-supported model and 95% confidence intervals that did not overlap 0.0. We feel this approach to model selection is appropriate for our study, because the habitat covariates we evaluated do not reflect mutually exclusive hypotheses, but rather each reflect individual non-exclusive factors that may affect male display site selection.

### **Acoustic Recordings**

We characterized male ruffed grouse drumming behavior using program Raven (Bioacoustic Research program 2014) to manually review each instance of drumming for each recorded male. From these data we quantified two distinct drumming metrics: drumming rate and wing beat rate. We recorded the total count of drumming events (drums) during each 1 hour period as the hourly drumming rate, where we defined a drum as a series of  $\geq 36$  wing beats in sequence. This insured that we only accounted for full drumming events and avoided observer error that may have occurred when counting wing beats within a drumming event. We further counted the total number of wing beats each male made while performing each full drumming event, which gave the wing beat rate for that drumming event. We used these two methods because we presumed they reflected different investments made by the male in reproduction; one related to the total male investment in display (drumming rate) and the other related to the male investment in each individual display (wing beat rate).

We compared each drumming activity metric to selected habitat covariates that we identified during our resource selection analysis using generalized linear mixed models (GLMMs) constructed in Program R. Under the GLMM framework, we included a random intercept term for each drumming stage in each year, which allowed us to account for repeated sampling of individual males and also to at least partially account for individual variation in

drumming behavior that was not related to any modeled fixed effects (Dingemanse and Dochtermann 2013). We performed a two-step approach for this analysis where we first constructed 5 single-variable models for each drumming response metrics, where we allowed drumming to vary by ordinal date, a quadratic effect of ordinal date, study area, year, and whether the male was radio-marked. We contrasted these models (which included the random intercept term) with a null model that contained only the random effect, as described above. This first step was necessary to test and account for possible confounding effects that could produce variability among recordings that were not related to habitat characteristics, and that we could account for in the models. For the second phase, we included a fixed additive effects as the supported habitat covariates from our RSF analysis, as well as variables supported in the first phase of the analysis. During this phase our null model included the supported variables from the first phase of analyses as well as the individual random intercept term. Model and variable support was determined as described above. For supported models we further estimated the proportional variance in each drumming metric that was associated with our GLMMs using the MuMIn package in Program R. This allowed for partitioning of the variance within our models by calculating both marginal and conditional  $R^2$  values, which provide an approximation of the variance attributed to the fixed effect alone and the combined fixed and random effects, respectively (Nakagawa and Schielzeth 2012). By subtracting marginal  $R^2$  from conditional  $R^2$ , we further obtained the approximate proportional variance explained by the random effect alone. These steps allowed us to better-understand which sources of variation (i.e. individual vs environmental) contributed to variability in ruffed grouse drumming behavior in general.

## Results

We located and sampled habitat characteristics at 72 used display locations (2015,  $n=39$ ; 2016  $n=33$ ) and at 144 random locations. Of the 72 used display stages 19 belonged to radio-marked males, and 30 of the used stages were located at Frye Mountain while 42 were located at Stud Mill Road. We evaluated 12 different habitat covariates at display locations, 7 of which performed above the null model (Table 2.1). However, a number of these models reflected the

Table 2.1. Resource selection function model results. Model selection results from generalized linear models comparing used display location of male ruffed grouse to available locations at two study areas in central Maine, U.S.A during the breeding season (April–June) 2015–2016.  $W_i$  is the model weight,  $K$  is the number of model parameters.

Model	$\Delta AIC_c$	$W_i$	$K$
Total Stem Density	0.00	0.59	2.00
Conifer Stems at 5m	2.29	0.19	2.00
Total Conifer Stem Density	3.71	0.09	2.00
Conifer Stems at 10m	3.92	0.08	2.00
Deciduous Stems at 5m	5.86	0.03	2.00
Total Deciduous Stems	9.11	0.01	2.00
Deciduous Stems at 10m	9.70	0.00	2.00
Null	10.55	0.00	1.00
Conifer Basal Area	10.99	0.00	2.00
Total Exotic Stem Density	11.12	0.00	2.00
Deciduous Basal Area	11.53	0.00	2.00
Total Basal Area	12.34	0.00	2.00
Visual Cover	12.90	0.00	2.00

same habitat characteristics measured at multiple scales (e.g. 5m vs 10m), and so we ultimately interpreted the characteristic at its best-supported scale. Male ruffed grouse selected display locations with greater total stem density around the display stage ( $\beta=0.52$ , 95% CI= 0.22-0.82; Fig. 2.1A) as well as greater conifer stem density within 5m of the display stage ( $\beta= 0.46$ , 95% CI= 0.17-0.75; Fig 2.1B).

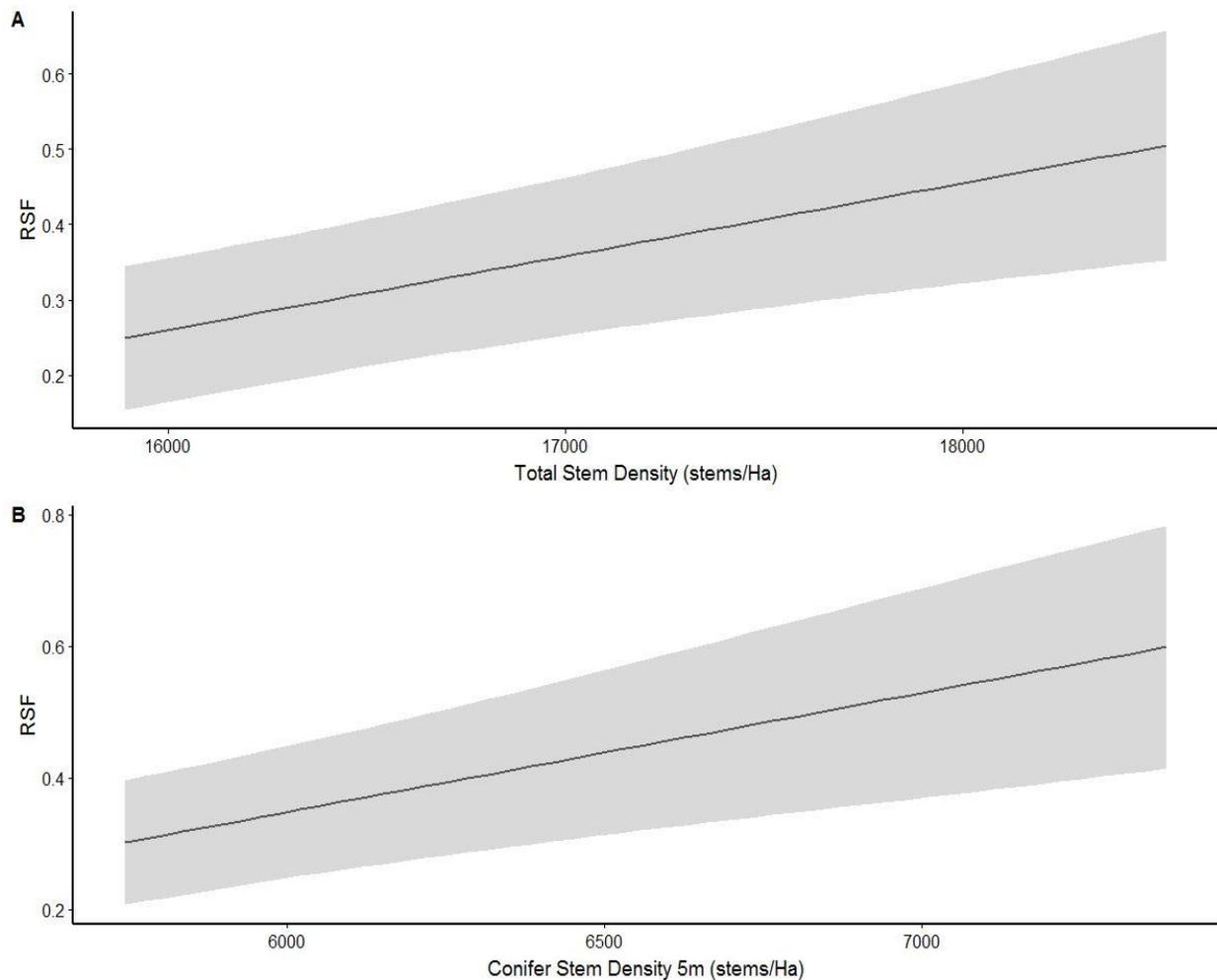


Figure 2.1. Resource selection function graphs. Selection of habitat characteristics by male ruffed grouse at display locations in two study area in central Maine, USA for spring 2015 and 2016. Ruffed grouse exhibited the greatest selection for A) woody stem density  $\leq 10$ -cm dbh, and B) conifer stem density within 5m from display stages. Stem densities were quantified using a 30-m belt transect perpendicular to the stage. Shaded areas represent 95% confidence intervals.

There was also support for selection of conifer stems at 10m and total conifer stems at display stages ( $\beta_{\text{conifer } 10\text{m}} = 0.42$ , 95% CI=0.14-0.70,  $\beta_{\text{total conifer}} = 0.43$ , 95% CI=0.14-0.72; Table 2.1), but

both of these covariates were highly correlated with the conifer stem density at 5m (Pearson's correlation=0.91 and 0.94, respectively), which was the scale that received the best support.

Deciduous stem density at 5m also performed better than the null ( $\beta = 0.37$ , 95% CI=0.09-0.65).

We did not find evidence to support selection or avoidance for visual cover, tree basal area (conifer, deciduous, or total), or exotic stems on selection (Table 2.1).

We documented drumming activity at 27 display stages (2015  $n=11$ ; 2016  $n=16$ ) with 324 hours of recorded audio between the two study areas. On average males drummed 6.4 times each hour, with a mean of 47.5 wing beats per drum. In phase 1 of analysis for wing beat rate, we

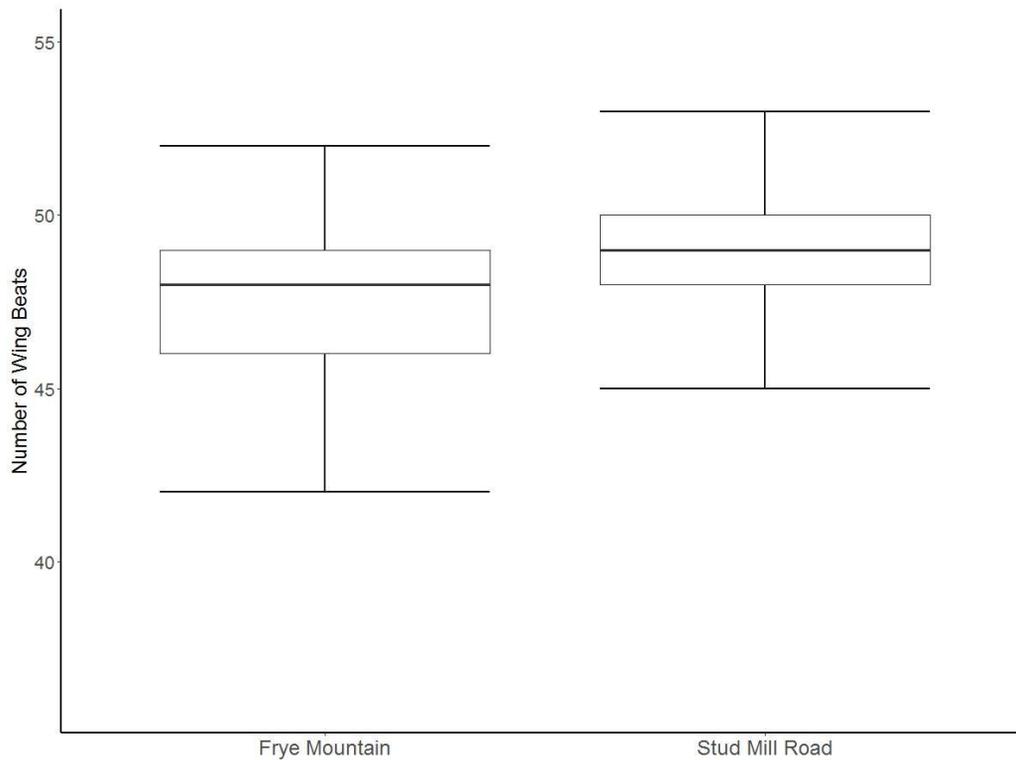


Figure 2.2. Wing beat differences between study areas. The average number of wing beats by male ruffed grouse during each drumming event for Frye Mountain and Stud Mill Road study areas in central Maine, U.S.A during April and May 2015–2016. Center lines indicate mean beats for the respective study area, boxes reflect 50% quantiles, and whiskers reflect 90% quantiles.

found support for a difference between study areas, where males at Stud Mill Road had more wing beats during each drum, on average, than males at Frye Mountain ( $\beta= 3.51$ , 95% CI= 1.50-5.52; Fig 2.2). In phase 2 of analysis, an additive effect of conifer stem density at 10m fell within 2.0 AICc of the study area model ( $\Delta\text{AICc}= 1.52$ ; Table 2.2); however, the 95% confidence intervals overlapped 0.0, indicating no conclusive support for this variable. The fixed effect of study area in our best-supported null model explained ~21% of the variance in male wing beat rate, and an additional 54% was explained by individual variation among males. For our

drumming rate model, a linear effect of ordinal date was the best-supported model during our first analysis, and in the second phase total stem density fell within 2.0 AICc of our ordinal date only model (null) ( $\Delta$  AICc=1.04; Table 2.2) but was not supported given 95% confidence that intervals overlapped 0.0. The fixed effect in our best-supported model for drumming rate (ordinal date) accounted for ~5% of the total variance, while individual variation among males accounted for an additional ~4% of the variance. We found no support for total stem density, conifer stems at 5m and 10m, total conifer stem density, or deciduous stem density at 5m for either drumming metric (Table 2.2; Fig. 2.3).

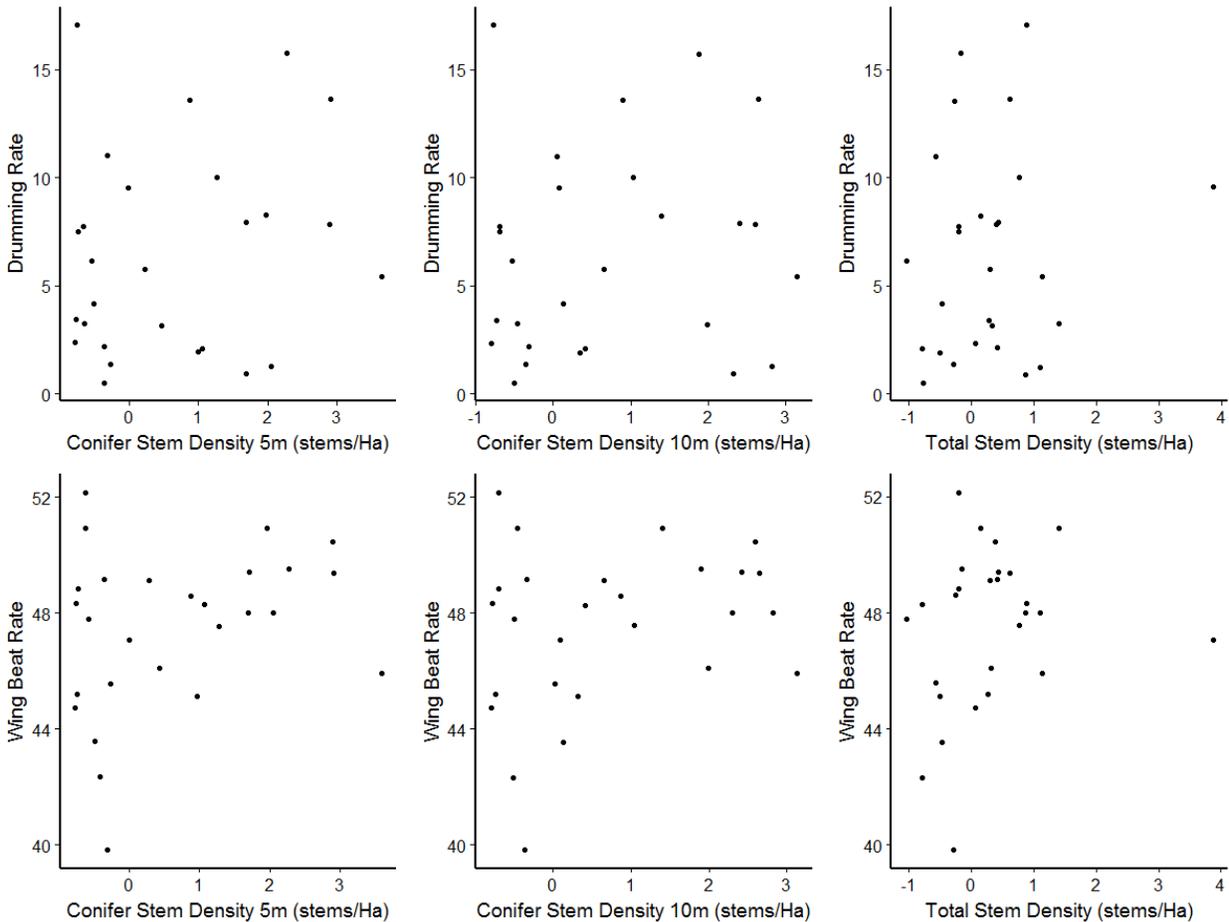


Figure 2.3. Drumming display scatterplots. Scatterplots representing two drumming variables: drumming rate (drum per hour) and wing beat rate (number of wing beats per drum) of male ruffed grouse in central Maine, U.S.A during April and May 2015–2016, compared to habitat covariates selected by male ruffed grouse at display locations.

Table 2.2. Display behavior model selection. Model selection results for covariate effects on display behaviors of male ruffed grouse at two study areas in central Maine, USA, during April–May, 2015 and 2016. For each of the individual analyses, the top performing variable from an initial phase of analysis was added as a fixed effect for all habitat variables.  $W_i$  is the model weight, and K is the number of model parameters.

<u>Model<sup>a</sup></u>	<u>AIC<sub>c</sub></u>	<u>ΔAIC<sub>c</sub></u>	<u><math>W_i</math></u>	<u>K</u>
<b>Drumming Rate</b>				
Ordinal Date	1048.07	0.00	0.27	4.00
Ordinal Date + Total Stem Density	1049.11	1.04	0.16	5.00
Ordinal Date + Conifer Stem Density 5m	1049.74	1.67	0.12	5.00
Ordinal Date + Conifer Stem Density 10m	1049.81	1.75	0.11	5.00
Null	1052.57	4.50	0.03	3.00
Year	1052.78	4.71	0.03	4.00
Study Area	1054.33	6.26	0.01	4.00
Radio-Marked Males	1054.65	6.58	0.01	4.00
<b>Wing Beat Rate</b>				
Study Area	6543.48	0.00	0.44	4.00
Study Area + Conifer Stem Density at 10m	6545.00	1.52	0.20	5.00
Study Area + Total Stem Density	6545.43	1.96	0.16	5.00
Study Area +Conifer Stem Density at 5m	6545.46	1.99	0.16	5.00
Ordinal Data	6550.89	7.41	0.01	4.00
Null	6551.16	7.69	0.01	3.00
Year	6552.00	8.53	0.01	4.00
Radio-Marked Males	6552.91	9.43	0.00	4.00

<sup>a</sup> Drumming Rate=Drums per hour; Wing Beat Rate=Number of wing beats per drum

## Discussion

We found evidence to suggest that total stem density and the composition of stem density (conifer vs. deciduous) at display locations were important habitat characteristics that affected display site selection; however, we did not find that selection for these habitat characteristics affected male drumming traits. It is possible that male ruffed grouse benefit from these habitat components in ways other than drumming performance. For instance, males may benefit from increased survival in the form of concealing habitat structure (Dessecker and McAuley 2001), access to necessary food resources to maintain energy requirements for the entirety of the breeding season (Gullion 1966), or an increase in reproductive success by selecting areas females

are drawn to without expending additional energy in drumming (Berkeley and Gutierrez 2017). For male ruffed grouse in Maine, it would seem as though conifer stem density is an important component at display stages, as we observed that males selected display locations that consisted of high stem density of conifers close to the stage compared to available locations.

Male ruffed grouse in this study selected for high total stem density at display locations and specifically selected for high conifer stem density within 5m of display sites. Previous studies disagree as to the role of forest composition (conifer versus deciduous) in ruffed grouse habitat. In general, ruffed grouse are commonly associated with early successional deciduous tree species, most notably aspen, which provides them with vital food resources and protective cover from predators (Gullion 1966), and it is generally thought that conifer trees are inferior to deciduous stems because they also provide protective concealment for avian predators. Berkeley and Gutierrez (2017) evaluated male drumming displays and the interactions with females and found no differences in male breeding success between the cover types. Our results are complementary in that we evaluated more fine-scale composition around display sites and did not find differences in breeding displays as a function of conifer vs. deciduous stem density. Although this ultimately reflects a null result, it also suggests that there was not a strong negative effect of conifer structure or cover on male display. This lends supporting evidence to a general conclusion that presence of conifers, even at relatively high densities, does not produce a negative consequence to males during the display period.

We did not find support for an effect of percent visual cover on drumming site selection. There has been some ambiguity among studies related to whether male ruffed grouse select display locations that have greater stem density (i.e. vertical structure) or greater shrub cover (horizontal cover providing visual obstruction) surrounding the stage, and it appears as though

these two habitat components are not selected together but rather males select one or the other (Palmer 1963, Boag and Sumanik 1969, Rusch and Keith 1971, Stoll et al. 1979, Zimmerman and Gutiérrez 2008, Hansen et al. 2011). Boag (1976) did an experimental study in Alberta where shrubs were removed at display stages and found that males abandoned stages where vegetation cover in the shrub level was removed. Conversely, Rusch and Kieth (1971) reported males used display stages that had lower density of shrubs and higher density of trees indicating an importance of canopy cover over ground cover. The difference in cover height and distance to display stages could be attributed to predator communities and different risk factors male ruffed grouse face throughout their range. As part of achieving a high fitness potential males select display stages that will promote reproductive success, and survival, both of which may vary across the ruffed grouse range and may also be affected by population density (Lovallo et al. 2000, Gaillard et al. 2010, Hansen et al. 2011). Regional differences may explain the variation among studies of habitat selected by males at display locations.

Additionally, we did not find that tree basal area affected selection, which suggests that birds did not avoid areas with larger, more mature trees. We further found that conifer basal area was neither selected nor avoided, suggesting that presence of mature conifers in the forest overstory did not affect selection at the scale we measured. Canopy cover is an important feature for ruffed grouse in that it provided protective overhead cover from avian predators, however, mature trees with broad canopies may also foster perches and concealment for avian predators to wait for unsuspecting prey (Boal et al. 2005, Zimmerman et al. 2007). We focused our analysis on a third order (within home-range) scale of selection, and variable support, or lack thereof, at one level of selection does not infer the same result at other levels (Johnson 1980, Jones 2001).

So, lack of evidence for support of these two variables may reflect selection that has already occurred at a higher level (i.e. selection of the home range; Johnson 1980).

We did not find a difference in display behavior or performance when compared to habitat covariates that were selected by male grouse at display locations. These results could have been influenced, in part, by our modest sample size and resulting lack of power associated with the recorded drumming activity during our study. Furthermore we could not account for a number of potential sources of heterogeneity among males at used display stages. Because the majority of our sample was comprised of unmarked males, we could not consider differences related to male age or body condition, which very likely affect display behaviors and performance of each male. Individual variation among displaying males is not well documented, as most drumming studies primarily incorporate unmarked males. In Minnesota, Gullion (1967) conducted a study of male ruffed grouse territory establishment and display stage usage and reported young males were more likely to comprise the non-drumming group for the first year before establishing a territory and display stage. Individual body condition could also affect a displaying male's behavior and performance, where males that have a higher body condition are able to expend more energy in display activity than males in lower condition. It has been documented that males can lose about one-half percent of their body weight each day during the 3 weeks of most intense display activity (Gullion 1984). We feel confident that used display stages were occupied by a dominant male, but we also had limited ability to account for events such as male replacement, death, or multiple males using the same stage. Our study increases the general knowledge of ruffed grouse drumming behavior by partitioning variance in drumming behavior metrics based on within- vs among-individual variation (Dingemanse and Dochtermann 2013). Specifically, we found that there was a moderate amount of variation in

wing beat rates among our two study areas, and greater than half of the variability in wing beat rate was associated with individual variability among males. In contrast, we were unable to explain much of any variance associated with drumming rates. This finding suggested that the rate of display may be a more random, and therefore less important, characteristic of male breeding display in ruffed grouse, when compared to the number of wing beats that males invest into each individual drum.

We found a difference between study areas and the number of times a male beat his wings during each drumming display, where male ruffed grouse had more wing beats per drum at Stud Mill Road than males at Frye Mountain. During an independent analysis, we also found that adult male ruffed grouse captured during August and September were in better body condition (mass corrected for body size) at Stud Mill Road compared to Frye Mountain (Davis et al. 2016 *unpublished analysis*). This spatial variation in body condition may explain the variation in wing beats per drum, in that males in better body condition should be capable of expending more energy in displays by increasing the number of wing beats in each drum. Other studies that have quantified male ruffed grouse displays using audio and visual recorders and have reported a range of wing beats per drumming display (40-50) along with directionality differences in drumming displays, but have not reported spatial differences (Aubin 1972, Garcia et al. 2012a, Berkeley and Gutierrez 2017). Additionally, one study found that variation in drumming displays was individually-specific and identifiable among males (Garcia et al. 2012b) but did not observe a significant difference in the number of wing beats among individuals. We documented a range of wing beats per drum (40-55) that were similar to other reported ranges of wing beats per drum (Aubin 1972, Garcia et al. 2012b). Producing more wing beats for every drumming event could

have fitness benefits in that more wing beats may be recognized by females as being a more physically fit individual, increasing male reproductive success (Gibson and Bradbury 1985).

## REFERENCES

- Aldridge, C. L., and M. S. Boyce. 2007. Linking Occurrence and Fitness to Persistence : Habitat-Based Approach for Endangered Greater Sage-Grouse. *Ecological Applications* 17:508–526.
- Archibald, H. L. 1976. Spring Drumming Patterns of Ruffed Grouse. *The American Midland Naturalist* 93:808–829.
- Aubin, A. E. 1972. Aural communication in ruffed grouse. *Canadian Journal of Zoology* 50:1225–1229.
- Banci, V., and G. Proulx. 1999. Resiliency of furbearers to trapping in Canada. *Mammal Trapping* 175–203.
- Barber, H. . 1961. The Ruffed Grouse. *Kentucky Happy Hunting Ground* 17:26–27.
- Bergerud, A. T., and M. W. Gratson. 1988. Survival and breeding strategies of grouse. Adaptive strategies and population ecology of northern grouse II:473–577.
- Berkeley, L., and R. Gutierrez. 2017. Display Behavior of Male Ruffed Grouse (*Bonasa Umbellus*) In Two Key Cover Types in Minnesota. *The Wilson Journal of Ornithology* 129:283–293.
- Bioacoustic Research program. 2014. Raven Pro: Interactive Sound Analysis Softward (version 1.5). The Cornell Lab of Ornithology, Ithaca NY.
- Blomberg, E. J. 2015. The influence of harvest timing on greater sage-grouse survival: A cautionary perspective. *Journal of Wildlife Management* 79:695–703.
- Blomberg, E. J., D. Gibson, J. S. Sedinger, M. L. Casazza, and P. S. Coates. 2013. Intra-seasonal variation in survival and probable causes of mortality in greater sage-grouse *Centrocercus urophasianus*. *Wildlife Biology* 19:347–357.
- Blomberg, E. J., J. S. Sedinger, D. Gibson, P. S. Coates, and M. L. Casazza. 2014. Carryover effects and climatic conditions influence the postfledging survival of greater sage-grouse. *Ecology and Evolution* 4:4488–4499.
- Blomberg, E. J., B. C. Tefft, J. M. Reed, and S. R. McWilliams. 2012. Evaluating spatially explicit viability of a declining ruffed grouse population. *Journal of Wildlife Management* 76:503–513.
- Boag. 1976. Influence of changing grouse density and forest attributes on the occupancy of a series of potential territories by male ruffed grouse. *Can. J. Zool* 54:1727–1736.
- Boag, D. A. 1976. The Effect of Shrub Removal on Occupancy of Ruffed Grouse Drumming Sites. *The Journal of Wildlife Management* 40:105–110.
- Boag, D. A., and K. M. Sumanik. 1969. Characteristics of Drumming Sites Selected by Ruffed Grouse in Alberta. *Journal of Ecology* 33:621–628.

- Boal, C., D. Andersen, and P. Kennedy. 2005. Foraging and Nesting Habitat of Breeding Male Northern Goshawks in the Laurentian Mixed Forest Province, Minnesota. *The Journal of Wildlife Management* 69:1516–1527.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281–300.
- Bumann, G. B., and D. F. Stauffer. 2002. Scavenging of Ruffed Grouse in the Appalachians: Influences and Implications. *Wildlife Society Bulletin* 30:853–860.
- Bump, G., R. W. Darrow, F. C. Edminster, and W. S. Crissey. 1947. *The Ruffed Grouse: Life History, Propagation, Management*. New York State Department of Environmental Conservation, New York.
- Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Second Addition. Springer-verlag, NY.
- Casas, F., A. Benítez-López, J. T. García, C. A. Martín, J. Viñuela, and F. Mougeot. 2015. Assessing the short-term effects of capture, handling and tagging of sandgrouse. *Ibis* 157:115–124.
- Davis, J. A. 1969. Aging and Sexing Criteria for Ohio Ruffed Grouse. *The Journal of Wildlife Management* 33:628–636.
- Davis, S. B., J. Mangelinkx, and E. J. Blomberg. 2016. Understanding population ecology of ruffed grouse inhabiting multiple use forest landscapes to inform habitat and harvest management.
- Dessecker, D. R., and D. G. McAuley. 2001. Importance of early successional habitat to ruffed grouse and American woodcock. *Wildlife Society Bulletin* 29:456–465.
- DeStefano, S., and D. H. Rusch. 1986. Harvest rates of ruffed grouse in northeastern Wisconsin. *Journal of Wildlife Management* 50:361–367.
- Devers, P. K., D. F. Stauffer, G. W. Norman, D. E. Steffen, D. M. Whitaker, J. D. Sole, T. J. Allen, S. L. Bittner, D. A. Buehler, J. W. Edwards, D. E. Figert, S. T. Friedhoff, W. W. Giuliano, C. A. Harper, W. K. Igo, R. L. Kirkpatrick, M. H. Seamster, H. A. J. Spiker, D. A. Swanson, and B. C. Tefft. 2007. *Ruffed Grouse Population Ecology in the Appalachian Region*. *Wildlife Monographs* 168:1–36.
- Dingemanse, N. J., and N. A. Dochtermann. 2013. Quantifying individual variation in behaviour: Mixed-effect modelling approaches. *Journal of Animal Ecology* 8:39–54.
- Ellison, L. N. 1991. Shooting and Compensatory Mortality in Tetraonids. *Ornis Scandinavica* 22:229–240.
- Fischer, C. A., and L. B. Keith. 1974. Population Responses of Central Alberta Ruffed Grouse to Hunting. *The Journal of Wildlife Management* 38:585–600.

- Gaillard, J.-M., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B. Van Moorter. 2010. Habitat-performance relationships: finding the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2255-2265.
- Garcia, M., I. Charrier, and A. N. Iwaniuk. 2012*a*. Directionality of the Drumming Display of the Ruffed Grouse. *The Condor* 114:500–506.
- Garcia, M., I. Charrier, D. Rendall, and A. N. Iwaniuk. 2012*b*. Temporal and Spectral Analyses Reveal Individual Variation in a Non-Vocal Acoustic Display: The Drumming Display of the Ruffed Grouse (*Bonasa umbellus*, L.). *Ethology* 118:292–301.
- Gibson, D., E. J. Blomberg, and J. S. Sedinger. 2016. Evaluating vegetation effects on animal demographics: The role of plant phenology and sampling bias. *Ecology and Evolution* 6:3621–3631.
- Godfrey, G. A., and W. H. Marshall. 1969. Brood break-up and dispersal of ruffed grouse. *Journal of Wildlife Management* 33:609–620.
- Gullion, G. 1965. Improvements in methods for trapping and marking ruffed grouse. *Journal of Wildlife Management* 29:109–116.
- Gullion, G. W. 1966. A Viewpoint concerning the Significance of Studies of Game Bird Food Habits. *The Condor* 68:372–376.
- Gullion, G. W. 1967. Selection and Use of Drumming Sites by Male Ruffed Grouse. *The Auk* 84:87–112.
- Gutierrez, R. J., G. S. Zimmerman, and G. W. Gullion. 2003. Daily survival rates of ruffed grouse *Bonasa Umbellus* in Northern Minnesota. *Wildlife Biology* 9:351–356.
- Hale, J. B., and R. S. Dorney. 1963. Seasonal Movements of Ruffed Grouse in Wisconsin. *The Journal of Wildlife Management* 27:648–656.
- Hannon, S. J., and K. Martin. 2006. Ecology of juvenile grouse during the transition to adulthood. *Journal of Zoology* 269:422–433.
- Hansen, C. P., M. A. Rumble, and J. J. Millsphaugh. 2011. Ruffed Grouse Selection of Drumming Sites in the Black Hills National Forest. *The American Midland Naturalist* 165:400–411.
- Johnson, D. H. 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology* 61:65–71.
- Jones, J. 2001. Habitat Selection Studies in Avian Ecology: A Critical Review. Source: *The Auk* 118:557–562.
- Kubisiak, J. F. 1984. The Impact of Hunting On Ruffed Grouse Populations in the Sandhill Wildlife Area. W. L. Robinson, editor.
- Kubisiak, J. F. 1989. Ruffed Grouse: Cluster drumming. E. S. Atwater and J. Schnell, editor.

- Laake, J. L. 2013. RMark: an R interface for analysis of capture-recapture data with Mark. AFSC Processed Rep.
- Lande, R. 1988. Genetics and Demography in Biological Conservation. *Science* 241:1455–1460.
- Larsen, J. a, and J. F. Lahey. 1958. Influence of weather upon a ruffed grouse population. *Journal of Wildlife Management* 22:63–70.
- Lindström, J. 1994. Tetraonid population studies — state of the art. *Annales Zoological Fennici* 31:347–364.
- Lovallo, M. J., D. S. Klute, G. L. Storm, W. M. Tzilkowski, M. J. Lovallo, D. S. Klute, and W. M. Tzilkowski. 2000. Alternate Drumming Site Use by Ruffed Grouse in Central Pennsylvania. *Journal of Field Ornithology* 71:506–515.
- Manly, B. F. J., L. L. McDonald, and D. L. Thomas. 1989. Resource selection functions. 14:268–272.
- Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. *Écoscience* 16:238–247.
- Nakagawa, S., and H. Schielzeth. 2012. A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Ecology and Evolution* 133–142.
- Nudds, T. D. 1977. Quantifying the vegetative structure of wildlife cover. *Wildlife Society Bulletin* 113–117.
- Palmer, W. L. 1963. Ruffed grouse drumming survey. *The Journal of Wildlife Management* 27:656–663.
- Pekkola, M., R. Alatalo, H. Pöysä, and H. Siitari. 2014. Seasonal survival of young and adult black grouse females in boreal forests. *European Journal of Wildlife Research* 60:477–488.
- Powell, L. A. 2007. APPROXIMATING VARIANCE OF DEMOGRAPHIC PARAMETERS USING THE DELTA METHOD : A REFERENCE FOR AVIAN BIOLOGISTS. *The Condor* 109:949–954.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Robinson, a C., R. T. Larsen, J. T. Flinders, and D. L. Mitchell. 2009. Chukar Seasonal Survival and Probable Causes of Mortality. *Journal Of Wildlife Management* 73:89–97.
- Rolland, V., J. A. Hostetler, T. C. Hines, H. F. Percival, and M. K. Oli. 2010. Impact of harvest on survival of a heavily hunted game bird population. *Wildlife Research* 37:392–400.
- Rusch, D. H., S. DeStefano, M. C. Reynold, and D. Lauten. 2000. *The Birds of North America*. Birds of North America, Inc, Philadelphia PA.
- Rusch, D. H., and L. B. Keith. 1971. Seasonal and Annual Trends in Numbers of Alberta Ruffed Grouse. *The Journal of Wildlife Management* 35:803–822.
- Sandercock, B. K. 2006. Estimation of Demographic Parameters from Live-Encounter Data: a Summary Review. *Journal of Wildlife Management* 70:1504–1520.

- Sandercock, B. K., E. B. Nilsen, H. Brøseth, and H. C. Pedersen. 2011. Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. *Journal of Animal Ecology* 80:244–258.
- Seather, B.-E., and O. Bakke. 2000. Avian Life History Variation and Contribution of Demographic Traits to the Population Growth Rate. *Ecology* 81:642–653.
- Skip, M. M., W. F. Porter, B. L. Swift, and M. V. Schiavone. 2011. Fall-Winter Survival of Ruffed Grouse in New York State. *Northeastern Naturalist* 18:395–410.
- Small, R. J., J. C. Holzward, and D. H. Rusch. 1991. Predation and hunting mortality of ruffed grouse in Central Wisconsin. *Journal of Wildlife Management* 55:512–520.
- Small, R. J., J. C. Holzward, and D. H. Rusch. 1993. Are Ruffed Grouse More Vulnerable to Mortality During Dispersal ? *Ecological Society of America* 74:2020–2026.
- Small, R. J., and D. H. Rusch. 1989. The Natal Dispersal of Ruffed Grouse. *The American Ornithologist* 106:72–79.
- Stoll, R. S., M. W. McClain, R. L. Boston, and G. P. Honchul. 1979. Ruffed Grouse Drumming Site Characteristics in Ohio. *Journal of Wildlife Management* 43:324–333.
- Svoboda, F. J., and G. W. Gullion. 1972. GROUSE USE OF ASPEN BY RUFFED MINNtESOTA. *The Journal of Wildlife Management* 36:1166–1180.
- Thompson, F. R., and E. K. Fritzell. 1988. Ruffed Grouse Winter Roost Site Preference and Influence on Energy Demands. *The Journal of Wildlife Management* 52:454–460.
- Thompson, F. R. I., and E. K. Fritzell. 1989*a*. Habitat Use , Home Range , and Survival of Territorial Male Ruffed Grouse. *The Journal of Wildlife Management* 53:15–21.
- Thompson, F. R. I., and E. K. Fritzell. 1989*b*. Habitat use, home range, and survival of territorial male ruffed grouse. *Journal of Wildlife Management* 53:15–21.
- Ward, H. G. M., P. J. Askey, and J. R. Post. 2013. A mechanistic understanding of hyperstability in catch per unit effort and density-dependent catchability in a multistock recreational fishery. *Canadian Journal of Fisheries and Aquatic Sciences* 70:1858.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.
- Yoder, J. M., E. A. Marschall, and D. A. Swanson. 2004. The cost of dispersal: Predation as a function of movement and site familiarity in ruffed grouse. *Behavioral Ecology* 15:469–476.
- Zimmerman, G. S., D. W. Gilmore, and R. J. Gutiérrez. 2007. Integrating Grouse Habitat and Forestry: An Example Using The Ruffed Grouse *Bonasa umbellus* in Minnesota. *Wildlife Biology* 13:51–58.
- Zimmerman, G. S., and R. J. Gutiérrez. 2008. Ruffed Grouse *Bonasa umbellus* habitat selection in a spatially complex forest: Evidence for spatial constraints on patch selection. *Ibis* 150:746–755.

## **BIOGRAPHY OF THE AUTHOR**

Samantha Davis was born in Montrose, Colorado, on February 15, 1990. She attend Montrose High School where she played on the women's soccer team and was an active member of the 4-H club. Samantha graduated high school in 2008 and attended her first year of college at Colorado Northwestern Community College. After her first year of college she transferred to New Mexico State University in Las Cruces, NM where she received her Bachelors in Agriculture majoring in Wildlife Ecology and Managment in 2012. Through a series of classes, technician positions, and volunteer activities that spanned avian ecology and plant community restoration, Samantha discovered her interest in avian ecology specifically associated with game bird ecology. Samantha is a candidate for the Master of Science degree in Wildlife Ecology from the University of Maine in August 2017.