

**Understanding population ecology of ruffed grouse inhabiting multiple use  
forest landscapes to inform habitat and harvest management**

**Final Technical Report**

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*Disclaimer: The findings contained in this report represent preliminary results of ongoing research; they should be cited as unpublished data until they have undergone peer review and publication.*

## ABSTRACT

Ruffed grouse are among the most popular game species in Maine, but information on the species' population ecology in the state has traditionally been lacking. Here we report on our results of data collected during a 3-year research project seeking to better understand ruffed grouse harvest, survival, reproduction, and habitat associations in Maine. In 2014 we established two study areas in central Maine; one at Frye Mountain Wildlife Management Area in Waldo County, and the second along the Stud Mill Road in Penobscot and Hancock Counties. During August and September 2014, 2015 and 2016, we captured 159, 99, and 61 unique ruffed grouse, respectively. Hunters harvested and reported 43 of 248 radio-marked ruffed grouse during 2014-2016 hunting seasons (October-December). We estimated a cumulative harvest rate of 0.16 (95% CI = 0.14-0.18). Harvest was greatest during the month of October and lower later in the season (Nov-Dec). Harvest rates were greater at Frye Mountain and were lower at Stud Mill Road (Frye Mountain  $H = 0.21$ ; Stud Mill  $H = 0.10$ ). Weekly survival probabilities for radio-marked ruffed grouse indicated lower survival of juveniles (< 1 year of age) compared to adults (>1 year of age). The mean annual survival of juveniles for this study was 0.13 ( $\pm 0.003$  SE), and the mean annual survival of adults was 0.28 ( $\pm 0.01$  SE). Seasonal survival was lowest for both age cohorts during fall and winter (October-March), and greatest during spring and summer (April-September). During spring and summer of 2015 and 2016 we located 72 drumming display stages of male ruffed grouse, collected 365 used summer locations of radio-marked birds, and monitored 15 broods with a brood success (proportion of broods with at least 1 chick 45 days post-hatch) of 57% for 2015 and 33% for 2016. During spring and summer 2015-2017 we located 45 nests and estimated cumulative nest success of 40.0%. Juvenile age ratios in the fall (juveniles per adult female in our fall captures) did not change appreciably during the study, and

were higher than those reported across much of the southern portion of the species' range. In contrast, annual survival, particularly of juvenile birds, was generally lower than many other published studies across the species' range. We speculate that the apparent declines in the grouse population that we observed during this study were related primarily to low survival, particularly of juvenile grouse in their first winter.

## **INTRODUCTION**

Ruffed grouse (*Bonasa umbellus*) are an important gamebird in Maine, with approximately half a million individuals harvested annually (MDIFW 2001). Ruffed grouse are associated with forests in early stages of plant succession (Dessecker and McAuley 2001), and so ruffed grouse populations are often closely linked with human land uses. Both commercial (timber harvest) and recreational (sport hunting) human activities may therefore affect ruffed grouse population dynamics, and abundance of ruffed grouse is likely to in turn affect public participation in sport hunting. Ruffed grouse are generally abundant in Maine (MDIFW 2001), but are declining throughout much of the eastern U.S. (Stauffer et al. 2011), including portions of New England (Blomberg et al. 2009, 2012).

Although ruffed grouse are managed as a game animal by the Maine Department of Inland Fisheries and Wildlife (MDIFW), little empirical research has been conducted on the species in the state. Published information on Maine ruffed grouse is generally sparse and largely related to nutritional ecology (e.g. Brown 1946, Servello and Kirkpatrick 1987) and disease (Eve and Davidson 1976). Accordingly, a number of fundamental questions related to grouse ecology that are specific to Maine's unique natural and cultural history remain unanswered (MDIFW 2001). MDIFW is consequently required to make population management decisions based on

information generated by seminal investigations in other states, and lacks contemporary information on annual survival rates, sources of natural and anthropogenic mortality, and harvest rates of ruffed grouse in Maine. Also, the relationship between forest management practices and ruffed grouse population performance is largely unexplored in Maine, but is likely to be affected by changes in forest products markets, silvicultural practices, agency habitat management, and non-commercial uses of privately owned forests (MDIFW 2001).

This project was initiated in 2014 as the first large-scale investigation of ruffed grouse population ecology in Maine. Our primary objectives were to quantify ruffed grouse harvest rates, evaluate seasonal and annual variation in ruffed grouse survival, measure components of reproduction (clutch size, nest success, chick survival), and evaluate characteristics of seasonal habitat use. Our study design relied primarily on radio-telemetry to monitor survival, reproduction, and habitat use of individual ruffed grouse, and we conducted our work at two study areas that differed in forest management objectives, general habitat composition, and ownership status.

This report summarizes our findings during the 3 years of this project highlighting our primary objectives and their results, as well as additional findings that fill in the geographical knowledge gap related to ruffed grouse ecology in Maine. In addition to previous progress reports, two graduate theses (Davis 2017, Mangelinckx 2017) were produced from this project that provide additional detail on data analyses, the results of these analyses, and further discussion of our findings and their implications. Citations to these and other communication products resulting from the project can be found in the Appendix 1 of this report.

## **METHODS**

### **Study Areas**

Our first study area was located on Maine Department of Inland Fisheries and Wildlife property in Waldo County, Maine, at Frye Mountain Wildlife Management Area (FM; Fig. 1). This area was ~5,200-acres of abandoned farm fields and upland forests that were managed specifically for ruffed grouse and American woodcock (*Scolopax minor*) through periodic clearcutting and field mowing. Northern hardwood stands dominated by maple (*Acer* spp.), birch (*Betula* spp.), white ash (*Fraxinus americana*), quaking aspen (*Populus tremuloides*), and American beech (*Fagus grandifolia*) were common. Balsam fir (*Abies balsamea*) was the most common conifer tree species, accounting for ~60% of the conifer basal area and ~39% of the total basal area at FM. Because this study area historically was occupied by agricultural homesteads, apple trees (*Malus domestica*) are commonly encountered on this landscape. Edge communities at FM are frequently dominated by the exotic and highly invasive shrub, Morrow's honeysuckle (*Lonicera morrowii*), although this species also can be found in interior forest. This study area was surrounded by private lands, comprised of maturing second-growth forest and some operational agricultural fields.

Our second study area was an area of commercial forest located in Penobscot and Hancock counties along a private forest road commonly referred to as the Stud Mill Road (SM; Fig. 1). It was an expansive area that contained a mixture of upland forest and wetlands. Partial cutting was the primary method of timber harvest used on this landscape. Common tree species in this study area included balsam fir, maple, birch, spruce (*Picea* spp.), eastern white pine (*Pinus strobus*), northern white cedar (*Thuja occidentalis*), and big-toothed aspen (*Populus grandidentata*). Balsam fir was the most common conifer species, representing ~44% of the

conifer basal area and ~32% of the total basal area at SM. Exotic shrub species have not been observed in this study area. At both SM and FM, the three most common herbaceous understory plants are Canada mayflower (*Maianthemum canadense*), starflower (*Trientalis borealis*), and bunchberry (*Cornus canadensis*).

### **Ruffed Grouse Capture**

During August and September 2014-2016, we trapped ruffed grouse using traps modified from the lily-pad design described by Gullion (1965), where approximately 20-m chicken wire fences directed ruffed grouse into wire funnels that led into round welded wire trap bodies with cloth mesh coverings. Traps were checked at least once daily throughout the trapping season, although in 2015 we increased check frequency to twice per day (late morning and evening) to reduce the frequency of self-inflicted injury. At initial capture we determined age as adult (>1 year of age) or juvenile (<1 year of age) and sex based on plumage characteristics (Davis 1969). We recorded individual mass (g) and the lengths (cm) of wing chord, tail, culmen, and tarsus, and fit each individual with an aluminum leg band stamped with a unique number. Most individuals were fitted 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 is increased by radio transmitters weighing >3% of a bird's body (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 phone number for hunters to report harvested ruffed grouse to the University of Maine Wildlife Demographics Lab.

## **Field monitoring**

Our strategy to monitor radio-marked ruffed grouse varied throughout the year. During the trapping seasons we checked live/dead status approximately daily to detect mortalities associated with capture and handling. We monitored radio-marked ruffed grouse at least weekly during the hunting season (October through December), once every 2 weeks from January through mid-April, and multiple times each week from May through July. Any time a radio-collar was heard in mortality mode, we recovered the collar and determined the probable cause of death. We classified cause of death as predation, harvest, or unknown, based on field evidence or hunter reporting. Ruffed grouse that survived longer than the maximum battery life of our radio transmitters, and radio-marked individuals that suddenly went missing, were presumed to have failed radios.

During mid-April and May of 2015 and 2016, we homed to the locations of male ruffed grouse 2-3 times each week shortly after sunrise, when drumming activity was highest, and attempted to locate display stages belonging to radio-marked males. We also located stages of unmarked males that we discovered incidentally. For our known display locations, we placed acoustic recorders at each for a 3-day period in an attempt to record male drumming behavior. We located and visually observed female radio-marked ruffed grouse 2-3 times per week during May and June. When we found a female in the same general area on consecutive visits, we flushed her to determine if she had a nest. If the nest was a plausible full clutch at discovery ( $\geq 9$  eggs for first attempts and  $\geq 6$  eggs for second attempts) we estimated the nest's stage of incubation using the egg flotation method presented by McNew et al. (2009). For incomplete clutches, we allowed females to finish laying before returning to record final clutch size and to estimate stage of incubation by egg flotation. We checked all nests for activity (i.e. presence of

the female) twice weekly by circling incubating females at a distance of >20-m. When a female left her nest, we inspected the contents of the nest bowl to determine nest fate, either success or failure, based on the condition of eggshell remains. Following successful hatch we located broods belonging to radio-marked females 1-2 times per week for 6-weeks post-hatch (hereafter brood locations), and flushed each brood once weekly from 2 to 5-weeks post-hatch to monitor brood survival. We flushed broods 3 times after the chicks reached 6-weeks to get a more reliable count of chick survival to 6- weeks of age. All males and females without broods (hereafter referred to as “non-reproductive”) were located by homing with radio-telemetry twice weekly during June and July. When homing, we approached radio-marked ruffed grouse until the signal strength from its radio transmitter indicated that we were ~20-m away from it. We circled to verify our distance estimate was correct, and recorded a waypoint using a handheld GPS unit and a bearing to the bird from that waypoint. We used this information to project the approximate coordinates of the bird’s specific location. This technique was used to limit the disturbance incurred by our bi-weekly acquisition of locations.

### **Vegetation Sampling**

During May and June, we measured vegetation characteristics at male display locations, and from mid-May through mid-August we measured vegetation characteristics at nest, brood, and non-reproductive locations used by ruffed grouse. In addition to measuring vegetation at these used location types, we measured vegetation at dependent random (DR) points that were located a random direction and distance (50-200-m) from the used location. The lower distance of 50-m was set to achieve some degree of independence between the used and random location, and the upper distance of 200-m was consistent with estimates of summertime mean daily movements by ruffed grouse observed by Small and Rusch (1989). We also measured vegetation



at independent random (IR) points that were located within the study area boundary. In 2015, we defined this distance at FM using the wildlife management area boundary. In 2016 at FM, and 2015-2016 at SM, we defined the distance by buffering our trap locations by 3.48-km, the mean ruffed grouse dispersal distance reported by Small and Rusch (1989). Point centers of random locations that fell in non-forest were moved to the nearest forest edge, which we defined as a location characterized by more or less extensive cover of tree species having woody stems taller than breast height.

We sampled 2 DR locations for each drumming display location, 2 DR and 1 IR location for each nest, and 1 DR and 1 IR location for each brood or non-reproductive location. At display locations, the plot center was defined as the display stage used by a drumming male, and at DR locations associated with display locations, we measured vegetation at the closest plausible display stage to the projected location. We defined the plausible display stage as logs greater than 10-cm in diameter and elevated off the ground (Hansen et al 2011). Plot center at nests was the center of the nest bowl, and the plot center at DR and IR locations associated with nests was the closest plausible nest-site to the projected points. We defined plausible nest-sites as locations positioned next to trees (i.e. dbh  $\geq$  10-cm), because ruffed grouse nests commonly have trees adjacent to and behind them (Bump 1947). At brood locations, the plot center was the point on the ground closest to the point from where the brood flushed. The plot center at non-reproductive location was the point on the ground closest to the projected location we obtained by homing, and plot centers of DR and IR locations associated with brood and non-reproductive locations was the point on the ground closest to the projected random DR or IR.

At all locations, we sampled tree basal area, visual obstruction, and woody stem density to assess local site structure and composition. Basal area (m<sup>2</sup>/ha) was measured using a 10-factor

wedge prism (Forestry Suppliers, Inc.) from the point center of each location. We recorded basal area by tree species, but for this report we aggregated to conifer and deciduous classes. To measure percent visual obstruction, we used a vegetation coverboard modified from Nudds (1977). Our coverboards were 25-cm tall by 25-cm wide, painted with a checkerboard of 5-cm x 5-cm red and white squares. With the coverboard at point center facing the observer the number of squares  $\geq 50\%$  visible were counted from a viewing distance of 3-m and a viewing height of 1-m. This was repeated for each of the cardinal directions. We subtracted the average number of visible squares from 25, then divided that number by 25 and multiplied by 100 to calculate a percent visible obstruction reading for each location.

We used belt transects where we counted all woody stems  $<10$ -cm dbh by class (i.e., deciduous, conifer, or exotic) within 1-m of the transect line to estimate woody stem density at each plot. At drumming stages we used a 30-m strip that ran perpendicular to the direction of the display stage. At nests, stems were counted in two 20-m strips that intersected at the nest and were oriented along the cardinal directions. At brood and non-reproductive locations, and random locations associated with those point types, we used a single 20-m strip that was oriented in a random direction to count stems. To convert stem counts to numbers of stems per hectare, counts were multiplied by 166.67 for display stages, 125 for nests, and 250 for brood, general, and random locations, with the differences reflective of the differing lengths of transects for each location type.

We estimated percent ground cover of forbs and *Rubus* at nests using 20-cm x 50-cm quadrat frames and the percent cover classes specified by Daubenmire (1959). Five frames were used at each nest, one centered on the nest and four 3-m out in each cardinal direction. The same was done at brood, non-reproductive, and random locations, except the frames were positioned at

5-m increments along the same 20-m transect line that was used for estimating stem density, with the 10-m frame placed over point center. Forb species richness was recorded in each frame. We averaged percent ground cover of forbs, *Rubus*, and forb species richness for each location for analyses.

## **Analytical Methods**

### *Annual and seasonal survival*

We estimated weekly survival probabilities for radio-marked ruffed grouse for the period 1 October 2014 to 28 February 2017 using nest survival models implemented in Program MARK (White and Burnham 1999). Nest survival analysis was chosen because it best-allowed for irregular monitoring of individuals, fitting our study design where frequency of monitoring varied throughout the year. We constructed models to analyze differences in survival based on temporal, spatial, and individual variables. Age, sex, study area, and year were included as group variables, and a weekly time scale was used to model various sources of seasonal variation in survival. We suspected hunting, winter, and nesting seasons to be periods of greater mortality for ruffed grouse because they are seasons of increased exposure to predators or periods of harsh weather 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 considered the seasonal structure as both an additive effect and as an interaction with other variables (e.g., Season\*Year).

Models were constructed in program R using the package “RMark” (Laake 2013). We used Akaike’s Information Criterion (AICc; Burnham and Anderson 2002) to assess model

support. We identified models having  $\Delta AIC \leq 2$  as well supported (Burnham and Anderson 2002). Variable support was further validated by examining beta estimates and evaluating whether 95% confidence intervals did not overlap zero. 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 press*). 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.

### *Harvest rates*

We estimated weekly and cumulative harvest rates for the 2014-2016 hunting seasons again using nest survival models implemented in Program MARK (White and Burnham 1999) and RMark (Laake 2013). 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. 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 mass on tarsus length, and used the residuals of that regression as estimates of size-corrected body mass (Blomberg et al. 2014). 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 (Williams et al. 2002).

#### *Over-winter survival*

We estimated over-winter weekly survival of radio-marked ruffed grouse for the period of 1 January to 31 March 2015-2017 using nest survival models implemented in Program MARK (White and Burnham 1999). We constructed models using program R (R Core Team 2013) to analyze differences in survival between study area, study year, age, sex, body condition, and environmental conditions (temperature, and snow depth). We used a weekly time scale to model various sources of intra-seasonal variation in survival and modeled additive and interactive effects among variables. Similar to our larger survival analysis, we also identified models having  $\Delta AIC \leq 2$  as well supported (Burnham and Anderson 2002) and further variable support was validated by examining beta estimates and evaluating that 95% confidence intervals did not overlap zero.

#### *Nest and female survival*

We estimated daily nest survival for the combined egg laying and incubation periods using nest survival models executed in Program MARK (White and Burnham 1999) and constructed in program R using the package “RMark” (Laake 2013). The models we ran represented our hypotheses regarding sources of variation in ruffed grouse nest survival. In addition to the six habitat covariates (Mangelinckx 2017), we evaluated differences in nest

survival between first nests and renests, age classes (females in their second or later nesting season vs females in their first nesting season), study year (2015-2017), and study areas (FM vs. SM). We also assessed if there were trends in nest survival by day of the nesting season, and the possible influence of time-varying weather covariates that corresponded to the day of the nesting season. We evaluated support for each covariate using the previously described criteria. We estimated cumulative nest survival (i.e. the probability a nest will hatch  $\geq 1$  egg) by raising daily nest survival probabilities to 35.44, which reflected the average length, in days, of the combined laying and incubation periods for ruffed grouse during our study.

Finally, we assessed whether the same set of covariates contributed to the survival of females during nesting. For this analysis, females that either successfully hatched nests, or whose nests failed but that survived, were right-censored from the survival history following their nest's fate. In that way, each female was alive and available for death due to predation until the fate of their nests. Hence, survival in this context reflects strictly female survival while nesting, and not female survival during the nesting season, per se. While female mortality contributes to total nest failure, there may be a different suite of factors influencing the mortality risk of nesting females. Therefore, the interpretation of these results were based solely on whether the covariates we investigated caused variation in female survival while nesting.

#### *Drumming site 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 location 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 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 characterized male ruffed grouse drumming behavior using program Raven (Bioacoustic Research program 2014) and manually reviewed each instance of drumming for each recorded male. From these data we quantified two distinct drumming metrics: drumming rate and 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. For supported models we 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.

### *Summer habitat selection and survival*

We evaluated differences in resource selection between brood-rearing females and non-reproductive ruffed grouse using resource selection functions (RSFs) that took the form of multinomial logistic regression models. Models were constructed using the package “nnet” (Venables and Ripley 2002) in program R (R Core Team 2013). Because we were interested in comparing used locations with available locations for both brood-rearing and non-reproductive individuals, but not interested in comparing the two types of available locations to each other, we ran separate analyses for landscape- and local-levels. Each analysis had 3 response categories: (1) available locations (either landscape- or local-level), (2) locations used by brood-rearing females, and (3) locations used by non-reproductive individuals. For the landscape-level analysis (i.e. Johnson’s [1980] 2<sup>nd</sup> order selection), we pooled use and locally-available random locations, and treated these collectively as “use” locations for comparison with landscape-level random locations. In doing so we assumed that use and locally-available locations collectively represented an area of probable seasonal use by each bird that occurred at the landscape level. To evaluate resource selection at the local-level (i.e. Johnson’s [1980] 3<sup>rd</sup> order selection) we compared each category of use locations to locally-available random locations. In both analyses, we applied a weighting to all observations, which adjusted each data point’s contribution to the



analysis based on the proportion of the total sample size represented by the location type. This helped to balance the analysis given that there were unequal number of replicates for each location type.

Prior to model building, we Z-standardized covariates and investigated correlations among them. We considered covariates with Pearson correlations  $>0.60$  as highly correlated, in which case we did not include them together in the same model. We used a two-step process to construct and run models to assess the importance of the ten covariates as components of summertime ruffed grouse habitat, and we repeated this process at each level of selection. In step one, we created a series of models where each included a single covariate, and we identified support for covariates when single term models performed better than the null models according to a criteria of 2.0 AICc (Burnham and Anderson 2002). We also validated covariate support by interpreting 85% confidence intervals of parameter coefficients (Arnold 2010), and considered covariates supported when intervals did not include zero. In the second step, we combined supported covariates from step one into a final, additive model, where in the case of highly correlated covariates we only included the covariate receiving the greatest support during step one. From these final models, we again interpreted parameter coefficients and associated confidence intervals to make inferences about life-stage-specific resource selection by ruffed grouse within our study areas. These inferences were based on the strength and direction of modelled effects between birds of both reproductive statuses, as well as relative differences in results between spatial levels of selection. We further evaluated the relative effects of specific resources on habitat selection by ruffed grouse using odds ratios that we derived from the beta coefficients of the final models, following the approach used by Doherty et al. (2008).

We estimated weekly survival probabilities for radio-marked ruffed grouse for the period 1 June to 16 August 2015-2016 using nest survival models implemented in Program MARK (White and Burnham 1999) constructed using the package “RMark” (Laake 2013) in program R. Models were constructed to evaluate hypothesized sources of variation in ruffed grouse summer survival using a two-step process. First, we modeled the effects of age and reproductive status on survival. We compared survival between second year (SY) and after-second-year (ASY) birds to differentiate between individuals in their first breeding season and those that had experienced at least one previous breeding season, and compared brood-rearing females to non-reproductive individuals to assess the effect of reproductive status on survival. Females that successfully hatched a nest were classified as “brood-rearing” until weekly flushes indicated brood loss, at which point they transitioned to “non-reproductive”. Females that failed to successfully hatch a nest and males were also classified as “non-reproductive”. We assessed the importance of age and reproductive status, separately and as additive effects in the same model, by comparison with an intercept-only null model using a criteria of 2.0 AICc. In the second step, we evaluated the influence of each habitat covariate on individual survival. We averaged resource measurements from all use location of each bird, and incorporated these covariates as individual additive effects into our best supported model from step one. Model and covariate support was assessed using previously described criteria. We calculated estimates of variance for weekly survival probabilities based on the Delta method (Powell 2007) using the package “emdbook” (Bolker 2016).

#### *Fall age ratios and body condition*

We used our fall capture data to evaluate two additional metrics related to ruffed grouse population performance: the ratio of juveniles to adult females captured in August and

September (hereafter age ratios) and the measured body condition of individuals in each sex/age class. Age ratios at capture provide a useful index to annual brood production, given that our capture period generally occurs after ruffed grouse are capable of independence but prior to or coincident with brood breakup and fall dispersal. We calculated age ratios as pooled estimates across both study areas, based on the number of unique individual ruffed grouse in each sex/age class (i.e. excluding recaptures), and assess changes in age ratios among study years. For this assessment we did not correct for differential detection probability among age- and sex-classes, and therefore we inherently assume that differences in detection probability were constant among our study years.

We defined individual body condition as the mass of each individual ruffed grouse, relative to its body size. This is a useful metric for demographic analysis because body condition can be an important predictor of individual survival (e.g. Blomberg et al. 2014), and can also be affected by environmental variation across space and time. We used data on mass and tarsus length to calculate body condition based on a linear regression, with mass as the response variable and tarsus length as the predictor. The residuals of the regression provided an estimate of size-corrected body mass, where a value of 0.0 reflects an animal in 'average' body mass, given its size, and where values above and below 0.0 reflect individuals in above- and below-average body condition, respectively. We used these residual terms as a response variable, and ran GLMs to evaluate whether ruffed grouse body condition varied among years, between study areas, and among age- and sex-classes. We also evaluated whether body condition changed with date during our 2-month fall capture season. We used similar approaches to model selection and evaluation of variable importance as described previously.

### *Comparison with other ruffed grouse population studies*

After three years of data collection, we are in a position to evaluate the population ecology of Maine ruffed grouse during 2014-2017 by comparing our demographic estimates to those published for the species across its range. We conducted a literature search for the following demographic rates: harvest rate, fall/winter and annual survival rates by age class, apparent nest success, renesting rate, clutch size for first and second nests, and fall age ratio. In the case of fall/winter survival rates, there was some variation in the literature with respect to the length of time included in a particular estimate (e.g., 5 vs. 6 months), so we normalized estimates from other studies to a monthly survival rate using the formula  $S_{\text{Month}} = SF/W^{(1/M)}$ , where M was the number of months included during any given study. In some cases, methodological differences among studies further complicate interpretation. For example, to our knowledge our study is the first to evaluate ruffed grouse nest success using modern approaches to nest survival analysis that account for differential detection of successful versus failed nests, which may vary significantly among studies and has long been recognized as a bias in studies of nesting ecology (Mayfield 1961; 1975). There is also a fairly large geographic discrepancy in when ruffed grouse research has been conducted across the species range, with the majority of work on core populations (e.g. the Upper Midwest and Canada) conducted prior to the 1990s, and the majority of work on southern/peripheral populations conducted more recently. Nevertheless, we believe it is useful and instructive to compare our results with those of past researchers, and we do so by classifying the range and median values of estimates present in the literature, and compare those with our estimates. We focused our search on citations contained within the Birds of North American Species Account for ruffed grouse (Rusch et al. 2000) and other works that have since been published.

## **RESULTS**

### *Descriptive results*

We captured a total of 335 individual ruffed grouse during our three-year study, of which 319 were captured in the fall and 16 were captured in the spring. During August and September of 2014, we captured a total of 159 unique ruffed grouse between the two study areas for a success rate of 2.1 grouse per 100 trap nights. Of these, 94 unique ruffed grouse were captured at FM, and 65 were captured at SM, 59 were adult males, 32 were juvenile males, 30 were adult females, and 37 were juvenile females (Table 1). Hunters harvested 17 of the 106 radio-marked ruffed grouse available for harvest during the 2014 hunting season. There were 25 mortalities during winter (January through March) of 2015, and 14 mortalities during spring and summer of 2015 (Table 2).

During the 2015 capture season, we captured a total of 99 unique ruffed grouse for a capture rate of 1.2 grouse per 100 trap nights. Of these 51 individuals were captured at Frye Mountain and 48 at Stud Mill, 28 were adult males, 33 were juvenile males, 19 were adult females, and 19 were juvenile females (Table 1). One hundred six radio-marked ruffed grouse were available for harvest at the beginning of hunting season 2015, and hunters harvested 21 of these by the end of the season. There were 14 additional mortalities during fall 2015, 16 radio-marked ruffed grouse mortalities occurred during winter 2016, and 21 mortalities during spring and summer 2016 (Table 2).

We captured 61 unique ruffed grouse during the 2016 capture season, resulting in a capture rate of 0.7 grouse per 100 trap nights. Of these, 42 were captured at Frye Mountain and 19 at Stud Mill, 9 were adult males, 21 were juvenile males, 14 were adult females, 15 were juvenile females, and 2 were juveniles of unknown sex (Table 1). Hunters harvested 5 radio-

marked ruffed grouse during the 2016 hunting season and 15 additional mortalities occurred during the fall, and 5 mortalities during the winter 2017 (Table 2).

We located and sampled vegetation at 72 used display locations (Table 3; 2015,  $n=39$ ; 2016  $n=33$ ) and 144 random locations between both study areas. Of the 72 used display stages, 19 belonged to radio-marked males, 30 of the stages were located at Frye Mountain while 42 were located at Stud Mill. During the summer 2015 and 2016 we sampled vegetation at 365 locations used by radio-marked ruffed grouse, including 288 locations used by 38 non-reproductive birds (males,  $n = 31$ ; females that failed to hatch nests,  $n = 3$ ; females that transitions to non-reproductive status after losing broods,  $n = 4$ ), and 77 locations used by 15 females with broods between both study areas. Of the 38 non-reproductive individuals, 10 were SY (second year) birds and 28 were ASY (after-second-year) birds, and of the 15 brood-rearing females, 4 were SY birds and 11 were ASY birds. We also sampled vegetation at 351 random locations available to ruffed grouse at the landscape-level, and 365 available locations at the local-level. Brood success across both years was 43.8%. In 2016, 4 brood loses were attributed to predation of the brooding female, in contrast to 2015 when no brooding females were predated. The average brood size at 6 weeks was 2.4 chicks/female in 2015 and 1 chick/female in 2016.

We monitored survival and measured habitat characteristics at both first and renests totaling 45 nests (2015  $n =16$  nests; 2016  $n =17$  nests; 2017  $n = 12$  nest; Table 3) belonging to 37 individual ruffed grouse. Of these, 34 were radio-marked females and 3 were unmarked females whose nests we found opportunistically. The average initiation date for first nests ( $n=32$ ) was April 28 ( $\pm 4.0$  SD) and the average hatch date was June 4 ( $\pm 3.5$  SD;  $n= 15$ ), whereas average renests ( $n= 13$ ) were initiated on May 24 ( $\pm 8.1$  SD) and hatched on June 27 ( $\pm 6.1$  SD;  $n= 9$ ). We did not find nests for 2 (5.6%) radio-marked females during our study, and we found second

nests within one nesting season for 8 out of 10 (80.0%) radio-marked females available to renest after their initial nests failed. The average completed clutch size of first nests ( $\bar{x} = 9.83 \pm 1.12$  SD) was greater than that of renests ( $\bar{x} = 6.77 \pm 1.59$  SD), and the average clutch size of first nests for females in their third year or later was  $9.95 (\pm 0.94$  SD) compared to  $9.56 (\pm 1.51$  SD) for females in their second-year. The average clutch size of renests for females in their third year or later was  $7.11 (\pm 1.05$  SD), and we observed only 2 renests belonging to females in their second year, each with 8 eggs.

#### *Annual and seasonal survival*

We included 248 unique ruffed grouse in our survival analysis, the majority (236) were caught during August and September, and 12 captured during the spring. Our best performing model of weekly survival included a monthly time structure with an additive effect of age (Table 4), which indicated juvenile ruffed grouse had a lower probability of survival than adults (Fig. 2B). Both age classes had the lowest survival probability during October and highest survival probability during July (Fig. 2A). The mean annual survival probabilities during our 3-year study for adults and juveniles were  $0.28 (\pm 0.01$  SE) and  $0.13 (\pm 0.003$  SE), respectively. We did not find support for effects of sex, study area, or year on survival (Table 4).

#### *Harvest rates*

When we considered all individuals that survived and were available for harvest during multiple years, our sample included 267 grouse/year combinations. Our top performing harvest models allowed survival to vary by week, with an additive effect of study area and age (Table 5). Survival was greater (i.e. lower likelihood of harvest) at Stud Mill than at Frye Mountain indicating higher harvesting rates at Frye Mountain (Fig. 3). For both Frye Mountain and Stud Mill, harvest rates declined as the season progressed (Fig. 3), with greater cumulative harvest

during October (Frye Mountain  $H_{\text{Oct}} = 0.14 \pm 0.02$  SE; Stud Mill  $H_{\text{Oct}} = 0.07 \pm 0.02$  SE) that was double that of the total harvest that occurred during November and December (Frye Mountain  $H_{\text{Nov-Dec}} = 0.07 \pm 0.02$  SE; Stud Mill  $H_{\text{Nov-Dec}} = 0.03 \pm 0.01$  SE). 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  $0.17 \pm 0.01$ ,  $0.19 \pm 0.01$ , and  $0.08 \pm 0.01$ , respectively, and the mean probability of an individual ruffed grouse being harvested during our study was 0.16 (95% CI = 0.14-0.18; Fig. 4). We did not find support for differences in harvest between sexes, among years, or based on individual body condition at time of capture (Table 5).

#### *Over-winter survival*

Our top performing model for our weekly winter survival had study area interaction with year, which indicated survival was lowest at Stud Mill  $0.94 (\pm 0.01$  SE) than at Frye Mountain  $0.98 (\pm 0.01$  SE) and that survival at both study areas increased with each study year. Weekly survival rates at Frye Mountain for winter 2015, 2016, and 2017 were  $0.97 \pm 0.01$ ,  $0.98 \pm 0.01$ , and  $0.99 \pm 0.004$ , and weekly winter survival rates for Stud Mill were  $0.92 \pm 0.02$ ,  $0.95 \pm 0.01$ , and  $0.98 \pm 0.01$ , respectively. We did not find significant support for an influence of weather conditions, age, or sex on survival during the winter.

#### *Nest and female survival*

We censored one nest from our survival analysis that failed due to apparent abandonment immediately after we flushed the female. Of the remaining 44 nests, 24 were successful and 20 failed. Twelve (60%) nests were destroyed by predators, where 4 nests had shell fragments in or around the nest bowl and 8 had no egg shell remains. Seven nests (35%) failed when the nesting female was killed, and 1 (5%) was abandoned for an unknown reason. In the latter case, we presumed abandonment was not related to our monitoring of the nest because the female was



observed on the nest and laid additional eggs after we flushed her from it. Nest survival models produced a mean daily survival rate for all nests over the course of our study of  $0.9745 \pm 0.0056$  SE, resulting in a cumulative nest survival probability of  $0.400 (\pm 0.008 \text{ 85\% CI})$ .

We found that coarse woody debris (CWD) was the only covariate that affected nest survival (Table 6). Nest sites with CWD nearby to the nest experienced lower success than nest sites without CWD near the nest ( $\beta = -0.410 \pm 0.332 \text{ 85\% CI}$ ), resulting in cumulative probabilities of success of  $0.269 (\pm 0.123 \text{ 85\% CI})$  and  $0.416 (\pm 0.139 \text{ 85\% CI}$ ; Fig. 5), respectively. We found no evidence that other habitat covariates affected nest survival, nor we did not detect variation in daily nest survival between first nests and re-nests, the two age classes of females, study years, study areas, or support for time trends in survival within the nesting season (Table 6). We also found no evidence that distance to nearest linear feature or any weather covariates influenced daily nest survival (Table 6).

We observed that 6 females were killed by predators during incubation of a first nest and 1 was killed during incubation of a re-nest. Four of these mortalities occurred in 2015, 3 occurred in 2016, and no mortalities occurred in 2017. The mean daily survival rate of females while nesting was  $0.9906 \pm 0.0035$  SE, which equated to a  $0.716 (\pm 0.005 \text{ 85\% CI})$  probability that a female ruffed grouse survived a single nesting attempt. Female mortality while nesting was associated with greater basal area ( $\beta = -0.632 \pm 0.472 \text{ 85\% CI}$ ) and greater conifer stem density ( $\beta = -0.333 \pm 0.223 \text{ 85\% CI}$ ) at nest sites. In addition, females whose nests had CWD nearby were 28.2% less likely to survive compared to females whose nest sites were without CWD ( $\beta = -1.057 \pm 0.778 \text{ 85\% CI}$ ; Fig. 5). We also found support for a negative relationship between distance to linear feature and females survival while nesting ( $\beta = -0.518 \pm 0.468 \text{ 85\% CI}$ ). Our results showed no indications that other habitat covariates affected daily survival of nesting

females, including horizontal visual obstruction, conifer basal area, or total stem density, and we also found no suggestion that nest initiation date, re-nest status, study area, study year, nesting female age, time trends within the nesting season, or weather affected survival of females while nesting. Additional results and interpretations relating to nest site habitat selection can be found in Mangelinckx 2017.

### *Drumming site selection*

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. 6A) as well as greater conifer stem density within 5m of the display stage ( $\beta= 0.46$ , 95% CI= 0.17-0.75; Fig 6B). There was also support for selection of conifer stems at 10m and total conifer stems at display stages ( $\beta_{\text{conifer 10m}}= 0.42$ , 95% CI=0.14-0.70,  $\beta_{\text{total conifer}}=0.43$ , 95% CI=0.14-0.72; Table 7), but both 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 7).

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 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). 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. 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. Additional results and interpretations relating to drumming behavior and habitat selection at display locations can be found in Davis 2017.

### *Summer habitat selection and survival*

Eight of the covariates we investigated influenced ruffed grouse habitat selection at the landscape-level (Table 8), and six met our requirements for inclusion into the final additive model for resource selection. Brood-rearing and non-reproductive ruffed grouse shared positive selection for areas with greater forb species richness and lesser deciduous basal area than available on the landscape (Table 9), and both life-stages neither selected nor avoided horizontal visual obstruction, ground cover by *Rubus*, or conifer stem density at the landscape-level (Table 9). However, the two groups differed in selection for stem density. Non-reproductive individuals selected areas on the landscape with greater stem densities, while brood-rearing females avoided those areas (Table 9, Fig. 7). Non-reproductive ruffed grouse were approximately two times more likely than brood-rearing females to use locations where stem density was 1 standard deviation greater than the mean (odds = 1.30, 85% CI = 1.05-1.61, and 0.68, 85% CI = 0.52-0.89, respectively; Table 9, Fig. 7). We did not detect selection for total basal area or tree density at the landscape-level for either reproductive status (Table 8).

At the local level, five habitat covariates were supported (Table 10) and all were included in a final, additive model for local-level resource selection (Table 11). Non-reproductive individuals again selected areas with greater stem densities, while brood-rearing females avoided locations with greater stem densities at the local level (Table 11) and were almost a third less likely (odds = 0.52, 85% CI = 0.33-0.81) as non-reproductive individuals

(odds = 1.46, 85% CI = 1.04-2.06) to use locations where stem density was a standard deviation greater than the mean (Fig. 7). Brood-rearing females selected locations with greater ground cover by *Rubus* (Table 11), and were about a quarter more likely to use locations where *Rubus* ground cover was a standard deviation greater than the mean (odds = 1.46, 85% CI = 1.14-1.88) compared to non-reproductive individuals (odds = 1.14, 85% CI = 0.87-1.50; Fig. 7). When combined with other variables in the final model, parameter coefficients gave no support for selection or avoidance of conifer stem density, proportion deciduous stems, and tree density by ruffed grouse at the local level (Table 11). In addition, we found no support for selection of forb ground cover, horizontal visual obstruction, forb species richness, deciduous basal area, or total basal area by ruffed grouse at either life-stage at this level (Table 10).

Our survival analysis showed that reproductive status and age were associated with individual variation in survival. Females with broods had a lower weekly survival probability ( $0.9551 \pm 0.0220$  SE) than non-reproductive individuals ( $0.9973 \pm 0.0027$  SE). This resulted in a 76% chance a female would survive to raise a brood to 6 weeks, whereas non-reproductive individuals had a 98% chance of surviving the same 6-week period. We found a positive effects of forb ground cover ( $\beta = 3.89 \pm 2.66$  85% CI) and negative effects of proportion deciduous stems ( $\beta = -1.64 \pm 1.24$  SE) on weekly survival. We found no support for effects of basal area, tree density, deciduous basal area, forb species richness, horizontal visual obstruction, or total stem density on summer weekly survival of ruffed grouse.

#### *Population size, fall age ratios and body condition*

Trapping success rates, expressed as individuals captured per 100 trap nights, provide an approximation of population change during the study. These values (2014 = 2.0; 2015 = 1.2; 2016 = 0.7) suggest a 40% decline in fall population size between 2014 and 2015, and an

additional 42% decline between 2015 and 2016. Based on unique individuals captured during August and September each year, the age ratio (juveniles per adult female) during each year of the study was 2014 = 2.3, 2015 = 2.7, and 2016 = 2.8. This relative stability in age-ratios despite large apparent population declines suggests that female success (number of young raised per adult female) was not a major driver of population decline. These relationships are visualized in Figure 8.

As expected, body size, as indexed by tarsus length, was a strong predictor of body mass ( $\beta=101.43 \pm 16.93$  SE). Body condition was also related to date of capture ( $\beta=1.60 \pm 0.19$  SE), with ruffed grouse captured later in the season having predictably higher body condition than early-caught birds. So, we included an ordinal date term in all models to account for this potentially confounding effect. After accounting for body size and date of capture, we found that body condition differed among male and female ruffed grouse (males were in greater condition;  $\beta=30.48 \pm 5.80$  SE), among adults and juveniles (juveniles were in lower condition;  $\beta = -71.06 \pm 7.71$  SE), and in general ruffed grouse were heavier for their size at the Stud Mill Road site ( $\beta=29.73 \pm 9.00$  SE; Table 12). We also found an interaction between study area and age class, which suggests that the difference in body condition between our study areas was driven primarily by the adult age class, and juvenile ruffed grouse were more similar in size between the two study areas (Fig. 9). Importantly, we found no evidence that body condition varied among our three study years (Table 12), suggesting that the population declines we observed throughout the study did not correlate with lower body conditions of birds prior to beginning of the fall/winter period.

### *Comparison with other ruffed grouse population studies*

We collected and summarized demographic estimates from 19 different ruffed grouse population studies, representing at least 26 distinct populations (Table 13), and compared the median and range of these values with estimates from our study (Fig. 10). Harvest during our study was lower than most range-wide estimates, fell within the bottom 25% of the range of published values (Fig. 10), and was most similar to values reported in New York (Skrip et al. 2011) and a number of sites throughout the southern Appalachians (Devers et al. 2007). Survival estimates for adult birds were similar (fall/winter) and slightly lower (annual) for Maine ruffed grouse during 2014-2016 when compared to range-wide estimates. For juvenile birds, the difference in survival rates was more pronounced, with both fall/winter and annual estimates substantially lower during 2014-2016 than range-wide median values (Fig. 10). We also found that apparent nest success (proportion of successful nests) was lower for our study than most range-wide estimates, however this difference should be interpreted cautiously because variation in field methods can produce large differences in estimates of apparent nest success among studies. Our estimates of female reneating rates were strikingly high compared to many range-wide estimates, particularly in contrast to values commonly reported for the southern Appalachians (Tirpak et al. 2006, Devers et al. 2007). We estimate that nearly all females established a second nest after loss of a first, whereas for many southern populations no such reneating was observed (Fig. 10). Our estimates of clutch size for Maine ruffed grouse, both for first and replacement clutches, are low relative to range-wide estimates, and are most similar to values reported throughout the southern Appalachians (Tirpak et al. 2006). However, the age-ratios that we observed during our fall captures were relatively high compared to range-wide

estimates, and were more than double the highest values reported during the six-year Appalachian Cooperative Grouse Research Project (Devers et al. 2007).

## **SUMMARY**

We estimated a mean cumulative harvest rate of 16% for ruffed grouse in Maine during the 2014-2016 ruffed grouse hunting seasons. This included all hunter reported-harvests, crippling losses, and presumed unreported harvests. Harvest was higher (nearly double) at Frye Mountain Wildlife Management Area and lower at the commercially-owned forests along the Stud Mill Road. We also found harvest rates were higher in October and lower later in the hunting season (Nov-Dec).

We found juvenile ruffed grouse had lower survival probabilities than adults, and seasonal survival of radio-marked birds was lowest during the fall and winter months and higher during the spring and summer months. Winter survival varied between study areas, with Stud Mill Road having a lower over-winter survival than Frye Mountain. Winter survival also varied among study years, where the first winter of our study had the lowest survival probabilities at both sites, and where survival increased progressively with each year. These increases in winter survival corresponded with a general decline in the ruffed grouse population, which is consistent with density dependence in over-winter survival. We did not find that temperature or snow depth during any given week affected survival during winter, but anecdotally conditions were most severe during the first winter of the study when survival was the lowest.

We found that approximately 40% of nests were successful during our 3-year study and the presence of coarse woody debris (CWD) at nest sites reduced overall nest survival. Females with nests that were associated with CWD experienced a 28.2% lower survival than females that nested in areas without coarse woody debris. Over all females experienced substantial mortality

while nesting, which equated to a 71.6% female survival rate during the average nesting period. In addition to the presence of CWD at nest sites, greater basal area and higher conifer stem density also contributed to lower female survival at nests. We found no evidence that other habitat characteristics, characteristics of nests themselves, or weather during nesting were related to nest survival or female mortalities.

We observed that ruffed grouse selected different components of habitat depending on their reproductive status and at differing landscape levels. 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 male breeding behavior. At the landscape-level during summer, non-reproductive ruffed grouse selected areas with greater stem densities, while brood-rearing females avoided these areas. Non-reproductive individuals further selected areas with greater stem densities at the local-level, while brood-rearing females again avoided areas with greater stem densities and selected locally-available areas with greater ground cover by *Rubus* at this scale. Weekly survival rates were reduced for brood-rearing females compared with non-reproductive individuals, which resulted in a 76% chance that a female would survive raising a brood to 6 weeks. In contrast, non-reproductive individuals had a 98% chance of survival over the same 6-week period. These differences likely reflect behavioral responses of individual ruffed grouse to alternative selective pressures at different life-history stages; specifically, males and non-reproductive females make habitat use decisions that improve self-maintenance and survival, whereas brood-rearing females select habitat with ample food resources for their broods at the expense of personal security. Overall female survival during



reproduction was low; during our study a hen had only a 54% chance of surviving both nesting and brood-rearing.

Understanding population dynamics and natural and anthropogenic stressors that affect populations is important when implementing species' management and conservation plans. Ruffed grouse are one of the most important game species in Maine. Although populations are considered abundant in Maine, there have been recent declines in southern parts of their range (Stauffer et al. 2011) and in portions of New England (Blomberg et al. 2012). As the first demographic study of ruffed grouse in Maine, our study takes important steps towards establishing foundational ruffed grouse research to inform management in the state.

As a whole, our findings paint a general picture of the population ecology of Maine ruffed grouse during 2014-2017. During this time period populations appeared to decline, as evidenced by our progressively lower trap success, and this observation is corroborated with anecdotal evidence from many ruffed grouse hunters who reported below-average bird numbers during the fall of 2016. While we found that harvest rates were relatively low, ruffed grouse survival rates, particularly those of juvenile grouse, were below-average during this time period. In contrast, female nesting and re-nesting effort was high, and the age-ratios we observed during trapping remained relatively constant across years. These results suggest that the apparent population declines we observed were likely driven by low survival, particularly during fall, winter, and spring. It is less likely that components of reproduction, such as nest success or chick survival, contributed to declines.

It is important to note that the demographic patterns we've observed are based on short-term data, and so they should be interpreted in the context of the conditions that occurred at our two study areas during the interval of our study. Future work should focus on understanding

more generally long-term dynamics of ruffed grouse populations in Maine, using a combination of citizen science datasets (e.g. Moose Hunter Surveys) and focused population surveys (e.g. Blomberg and Martin 2015). This would permit a better understanding of the periodicity and frequency of growth/decline in Maine's ruffed grouse populations, and place short-term declines in a larger context.

We found that ruffed grouse harvest rates in Maine were lower than many reported estimates within the species' range. The majority of harvest occurred early in the season during the month of October, with comparably less late-season harvest. While our study design doesn't allow us to directly evaluate evidence for additive versus compensatory mortality of ruffed grouse in Maine, the patterns in survival and harvest we observed are most consistent with compensatory mortality. Harvest rates were higher at Frye Mountain WMA, but over-winter mortality was lower at that site and we found no difference in annual survival probability between the two study areas. We also found that over-winter survival increased as population size decreased, which is consistent with density-dependence in survival; a pre-requisite for compensatory mortality. Finally, the survival rates we observed are lower than those reported by Devers et al. (2007), who demonstrated compensatory mortality in ruffed grouse via experiment. Overall our results suggest that current harvest practices in Maine are consistent with sustainable harvest of ruffed grouse populations.

## **COMMUNICATION PRODUCTS**

Whenever possible we communicated the progress of the project and our results with a variety of audiences, from wildlife professionals to the general public. To date we have conducted 10 public outreach events, our research has been featured by the state press on radio and print media 6 times, we have written 6 technical reports, and we have given 18 professional

presentations on aspects of the project, including 5 that were delivered at the 2016 conference of The Wildlife Society. Two graduate student theses have been published, and 3 manuscripts have been submitted for peer-reviewed publication in scientific journals. We include a list of all communication products as Appendix 1.

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Table 1. Unique ruffed grouse captures, by age and sex cohort, at two study areas in central Maine, USA during August and September 2014 and 2016, and August through mid-October 2015. Birds were captured at Frye Mountain Wildlife Management Area (FM) and Stud Mill Road commercial forest (SM).

	Adult Males	Adult females	Juvenile males	Juvenile females	Total captures
2014					
FM	42	22	16	13	94
SM	17	8	16	24	65
Total	59	30	32	37	159
2015					
FM	17	15	8	14	54
SM	11	4	25	5	45
Total	28	19	33	19	99
2016					
FM	5	11	16	9	<sup>a</sup> 42
SM	4	3	5	6	19
Total	9	14	21	15	61

<sup>a</sup> 2 juveniles of unknown sex were captured at FM.

Table 2. Cause-specific mortalities of radio-marked ruffed grouse, by season, from two study areas in central Maine, 1 October 2014 to 30 September 2016. Harvest mortality occurred only during the fall hunting season, October 1 to 31 December each year.

Season <sup>a</sup>	Avian	Mammal	Unknown Predator	Unknown Cause	Harvest <sup>b</sup>	Total Deaths
2014-2015						
Fall	8	10	2	5	17	42
Winter	13	5	2	5	-	25
Spring	8	2	0	2	-	12
Summer	1	1	0	0	-	2
2015-2016						
Fall	6	1	1	6	21	35
Winter	4	4	4	4	-	16
Spring	7	3	3	1	-	14
Summer	5	1	0	1	-	7
2016-2017						
Fall	6	6	2	1	5	20
Winter	1	1	2	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 those that were shot and not recovered.

Table 3. Number of used locations where vegetation was measured at two study areas in central Maine, USA. These data were collected during the spring and summer of 2015, 2016 for all location types, and also during 2017 for nests, and are arranged by location type.

Study area <sup>a</sup>	Non-reproductive	Brood	Drumming stage	Nest
2015				
FM	79	24	13	12
SM	76	9	26	4
2016				
FM	67	37	17	15
SM	67	6	16	2
2017				
FM	-	-	-	7
SM	-	-	-	5
Total	289	76	72	45

<sup>a</sup> FM = Frye Mountain Wildlife Management Area; SM = Stud Mill Road commercial forest.

Table 4. Model selection results for weekly survival analysis of radio-marked ruffed grouse at 2 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).

Table 5. Model selection results for weekly harvest analysis of radio-marked ruffed grouse at 2 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.

Models <sup>a</sup>	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).

Table 6. AICc table for nest survival. Model selection results for daily nest survival of ruffed grouse at two study areas in central Maine, USA, from April 21-July 8, 2015-2017. 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.

Model	$\Delta\text{AICc}^a$	$W_i$	$K$
Coarse woody debris	0.00	0.17	2
NULL	1.24	0.09	1
Initiation date	1.37	0.08	2
Renest	1.71	0.07	2
Conifer stem density	1.92	0.06	2
Basal area	1.95	0.06	2
Horizontal visual obstruction	2.29	0.05	2
Distance to linear feature	2.45	0.05	2
Nesting female age	2.71	0.04	2
Year	2.86	0.04	2
Time trend	2.87	0.04	2
Total stem density	2.95	0.04	2
Maximum daily temperature	2.95	0.04	2
Precipitation	3.15	0.03	2
Conifer basal area	3.19	0.03	2
Minimum daily temperature	3.21	0.03	2
Study area	3.24	0.03	2
Time trend quadratic	3.36	0.03	2

<sup>a</sup> Lowest AICc = 144.56.

Table 7. Model selection results from generalized linear models comparing used display locations 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

Table 8. AICc table for landscape-scale summer resource selection. Model selection results from multinomial logistic regression models comparing locations used by ruffed grouse (non-reproductive:  $n = 288$ , brood:  $n = 77$ ) to landscape-level available locations ( $n = 351$ ) at two study areas in central Maine, USA, late-May through early-August of 2015 and 2016.  $\Delta\text{AICc}$  is the difference in AICc from the top model,  $W_i$  is the model weight, and  $K$  is the number of model parameters. The Full Model includes all variables that were better supported than the Null model, based on AICc.

Model	$\Delta\text{AICc}^a$	$W_i$	$K$
Full Model	0.00	1.00	14
Total stem density	13.13	0.00	4
Forb species richness	16.52	0.00	4
Proportion deciduous stems	19.14	0.00	4
Conifer stem density	23.84	0.00	4
Forb ground cover	30.66	0.00	4
<i>Rubus</i> ground coverage	31.81	0.00	4
Horizontal visual obstruction	33.14	0.00	4
Deciduous basal area	34.05	0.00	4
NULL	34.90	0.00	2
Basal area	37.08	0.00	4
Tree density	37.81	0.00	4

<sup>b</sup> Lowest AICc = 984.23.



Table 9. Coefficients from landscape-scale Full Model. Parameter coefficients with 85% confidence intervals (LCL and UCL) from the final additive multinomial regression model. Only covariates that performed better than the null model according to AICc were included. This analysis compares locations used by radio-marked ruffed grouse to landscape-level available locations. Data were collected within two study areas in central Maine, USA, late-May through mid-August of 2015 and 2016.

Parameter	Brood-rearing vs landscape			Non-reproductive vs landscape		
	Estimate	LCL	UCL	Estimate	LCL	UCL
Intercept	-0.10	-0.29	0.08	0.04	-0.13	0.21
Total stem density	-0.38	-0.65	-0.12 *	0.26	0.04	0.48 *
Forb species richness	0.46	0.27	0.65 *	0.36	0.17	0.55 *
Conifer stem density	-0.25	-0.54	0.03	-0.09	-0.30	0.11
<i>Rubus</i> ground cover	0.16	-0.03	0.34	-0.05	-0.24	0.15
Horizontal visual obstruction	-0.05	-0.24	0.14	-0.11	-0.29	0.08
Deciduous basal area	-0.19	-0.37	-0.02 *	-0.20	-0.37	-0.02 *

\* Denotes 85% confidence interval that does not include zero.

<sup>a</sup> All covariates were Z-standardized prior to analysis. Total stem density:  $\bar{x} = 9618.41$  stems/ha, SD = 7935.13 stems/ha; Forb species richness:  $\bar{x} = 1.28$  species, SD = 0.86 species; Conifer stem density:  $\bar{x} = 3588.11$  stems/ha, SD = 4954.03 stems/ha; *Rubus* ground cover:  $\bar{x} = 3.1\%$ , SD = 6.7%; Horizontal visual obstruction:  $\bar{x} = 61.6\%$ , SD = 28.6%; Deciduous basal area:  $\bar{x} = 10.26$  m<sup>2</sup>/ha, SD = 9.16 m<sup>2</sup>/ha.

Table 10. AICc table for local-scale summer resource selection. Model selection results from multinomial logistic regression models comparing locations used by ruffed grouse (non-reproductive:  $n = 288$ , brood:  $n = 77$ ) to locally available locations ( $n = 365$ ) at two study areas in central Maine, USA, late-May through early-August of 2015 and 2016.  $\Delta\text{AICc}$  is the difference in AICc from the top model,  $W_i$  is the model weight, and  $K$  is the number of model parameters. The Full Model includes all variables that were better supported than the Null model, based on AICc.

Model	$\Delta\text{AICc}^a$	$W_i$	K
Full Model	0.00	0.99	12
Total stem density	10.72	0.00	4
Conifer stem density	13.84	0.00	4
Proportion deciduous stems	14.69	0.00	4
Rubus ground cover	19.59	0.00	4
Tree density	24.10	0.00	4
NULL	25.56	0.00	2
Forb ground cover	26.66	0.00	4
Forb species richness	26.95	0.00	4
Horizontal visual obstruction	27.08	0.00	4
Basal area	29.00	0.00	4
Deciduous basal area	29.16	0.00	4

<sup>b</sup> Lowest AICc = 486.02.

Table 11. Coefficients from local-scale Full Model. Parameter estimates with 85% confidence intervals (LCL and UCL) from the final additive multinomial regression model. Only covariates that performed better than the null model according to AICc were included. This analysis compares locations used brood-rearing and non-reproductive radio-marked ruffed grouse to locally available locations. Data were collected during late-May through mid-August of 2015 and 2016 at two study areas in central Maine, USA.

Parameter	Brood-rearing vs local				Non-reproductive vs local		
	Estimate	LCL	UCL	*	Estimate	LCL	UCL
Intercept	-0.28	-0.55	-0.01	*	-0.04	-0.28	0.20
Total stem density	-0.66	-1.12	-0.21	*	0.38	0.04	0.72 *
<i>Rubus</i> ground cover	0.38	0.13	0.63	*	0.13	-0.14	0.41
Conifer stem density	0.01	-0.63	0.64		-0.09	-0.50	0.33
Proportion deciduous stems	0.28	-0.13	0.69		-0.13	-0.51	0.25
Tree density	-0.12	-0.41	0.16		0.18	-0.07	0.43

\* Denotes 85% confidence interval that does not include zero.

<sup>a</sup> All covariates were Z-standardized prior to analysis. Total stem density:  $\bar{x} = 9618.41$  stems/ha, SD = 7935.13 stems/ha; *Rubus* ground cover:  $\bar{x} = 3.1\%$ , SD = 6.7%; Conifer stem density:  $\bar{x} = 3588.11$  stems/ha, SD = 4954.03 stems/ha; Proportion deciduous stems:  $\bar{x} = 0.60\%$ , SD = 0.35%; Tree density:  $\bar{x} = 2761.84$  trees/ha, SD = 1337.99 trees/ha.

Table 12. Model selection results from generalized linear model evaluating variation in size-corrected body mass among age- and sex-classes, study sites, and years. Data are from birds captured during August and September, 2014-2016, and include only newly-captured individuals (N=313). 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.

Model <sup>a</sup>	AICc	$\Delta$ AICc	$W_i$	$K$
Sex + Age*Site	3353.16	0.00	0.61	6
Sex + Age + Site	3354.22	1.06	0.36	5
Sex + Age + Year	3360.57	7.41	0.02	5
Sex + Age	3360.93	7.77	0.01	4
Sex + Age*Year	3363.51	10.35	0.00	6
Age	3386.22	33.06	0.00	3
Sex	3489.44	136.28	0.00	3
Null	3510.99	157.82	0.00	2
Site	3512.95	159.79	0.00	3
Year	3514.55	161.38	0.00	4

<sup>a</sup>We included an ordinal date term in all models to account for the progressive increase in body

Table 13. Summary of ruffed grouse vital rates obtained from published literature. A comparison with our estimates for Maine ruffed grouse is shown in Figure 10.

Rate	Minimum	Mean	Median	Maximum	SD	No. Studies
Harvest Rate	0.06	0.24	0.23	0.46	0.12	13
Fall-Wint. Survival (Adult) <sup>b</sup>	0.85	0.89	0.89	0.94	0.03	11
Annual Survival (Adult)	0.11	0.37	0.38	0.57	0.12	14
Fall-Winter Survival (Juv) <sup>b</sup>	0.80	0.89	0.89	0.95	0.04	8
Annual Survival (Juv)	0.08	0.33	0.35	0.52	0.13	8
Nest Success (Apparent)	0.48	0.62	0.63	0.88	0.13	10
Renest Rate <sup>c</sup>	0.00	0.13	0.00	0.31	0.16	7
First Clutch Size	8.89	10.57	10.68	12.80	1.07	12
Second Clutch Size	6.67	7.24	7.35	7.60	0.35	8
Fall Age Ratio (J:AF)	0.24	0.82	0.47	4.00	1.00	13

<sup>a</sup> Estimates obtained from the following sources: DeStefano and Rusch 1984, Rusch et al. 1984, Kubisiak 1984, Thompson and Fritzell 1989, Small et al. 1991, additional citations contained in Rusch et al. 2000, Gutierrez et al. 2003, Tirpak et al. 2006, Devers et al. 2007, Skrip et al. 2011.

<sup>b</sup> Fall-Winter survival reported as a monthly probability.

<sup>c</sup> Proportion of hens attempting a second clutch given loss of a first nest.

<sup>d</sup> Age ratio reported as juveniles per adult female.

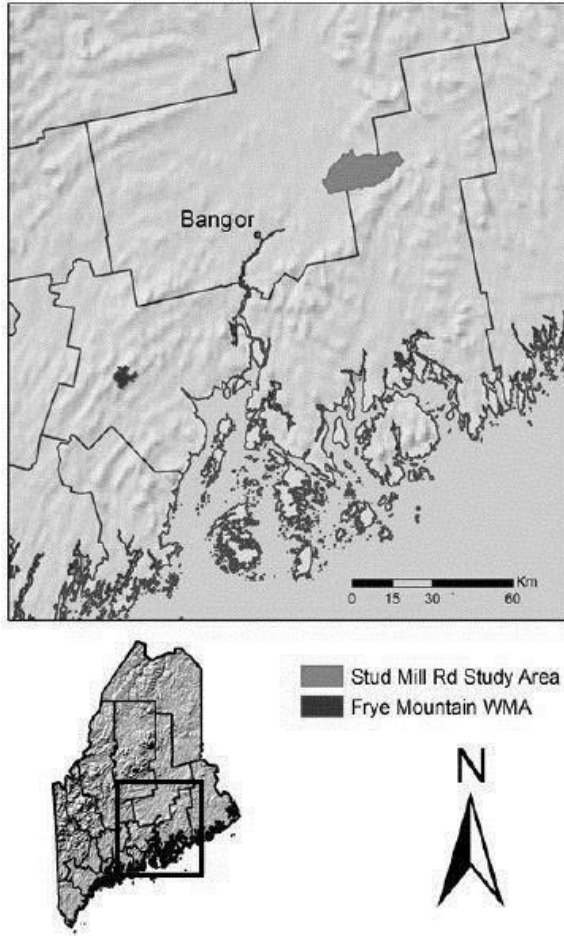


Figure 1. Locations of ruffed grouse study areas in central Maine, USA. Frye Mountain Wildlife Management Area is shown in dark gray, whereas the Stud Mill Road commercial forest is shown in medium gray. The extent of the study areas are depicted in the top map, shown within the map of Maine below.

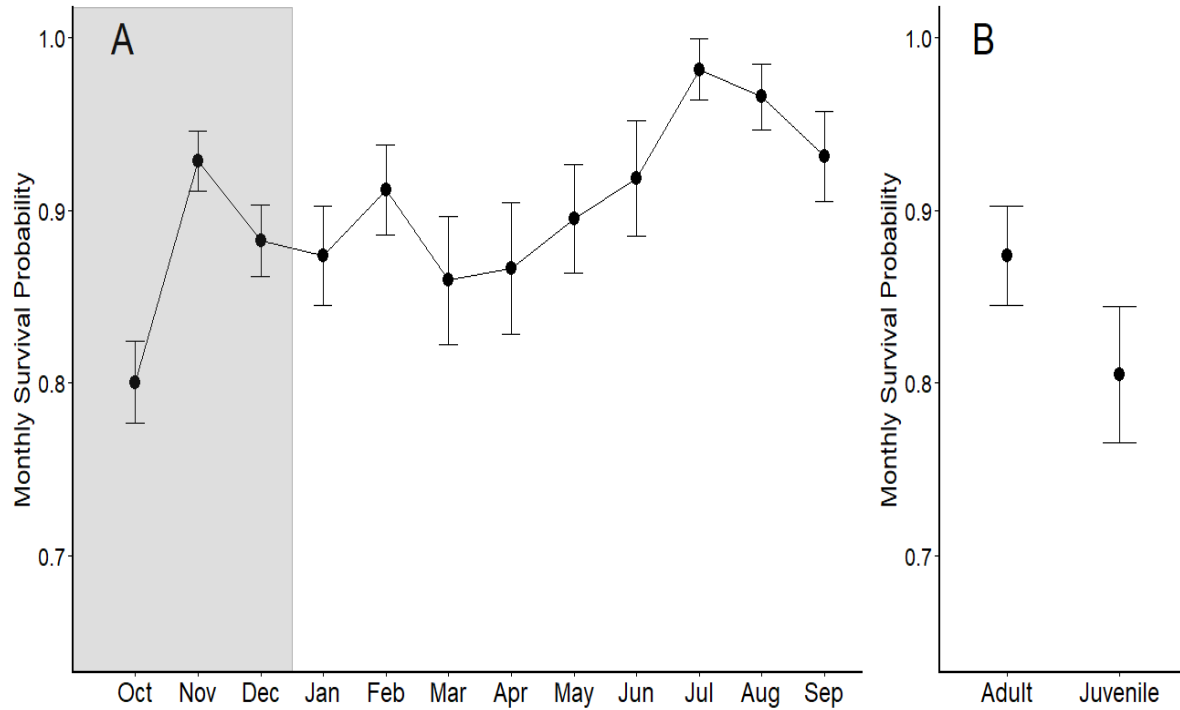


Figure 2. Monthly survival probabilities of A) adult (>1 year of age at capture) radio-marked ruffed grouse during 2014–2016 in central Maine, USA, and B) difference in monthly survival estimates survival between adult and juvenile (<1 year of age at capture) ruffed grouse. Estimates were derived from the most competitive model (Table 2), where survival varied by month with an additive effect of age. For panel 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).

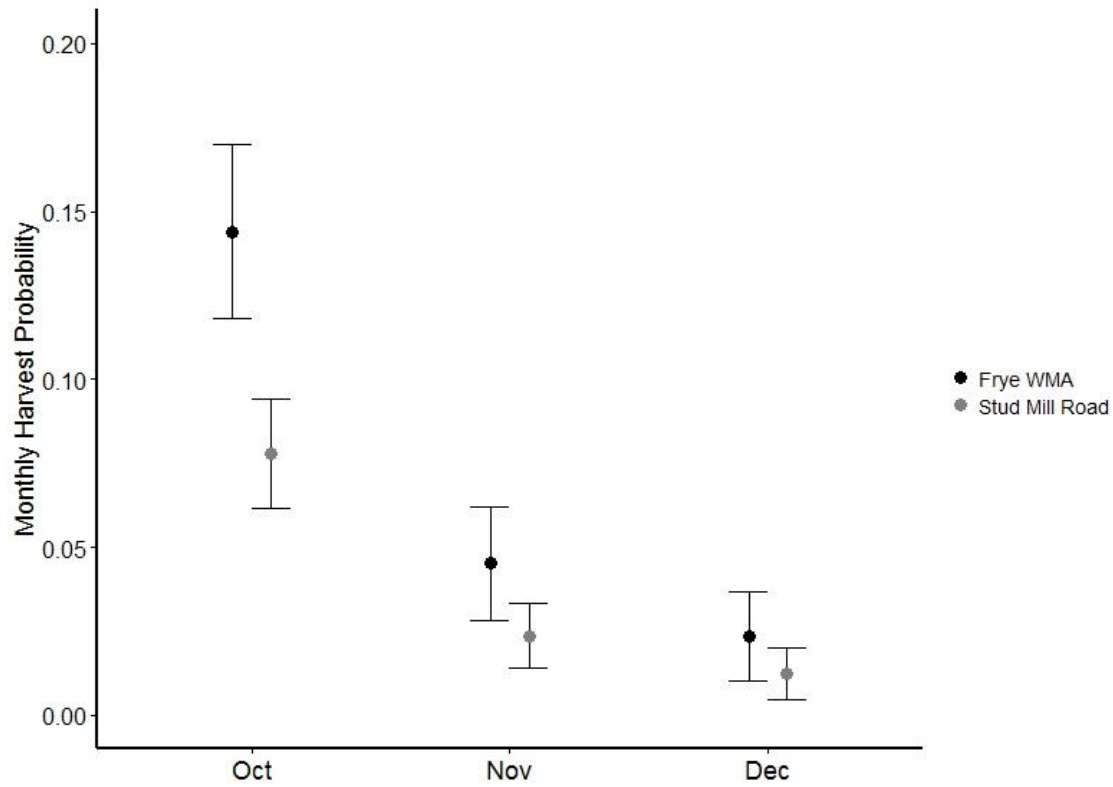


Figure 3. Monthly harvest probabilities of radio-marked ruffed grouse between 2 study areas in central Maine, USA. Estimates were derived from the most competitive model (Table 5), which included a fixed effect of study area. Error bars reflect standard error (SE).



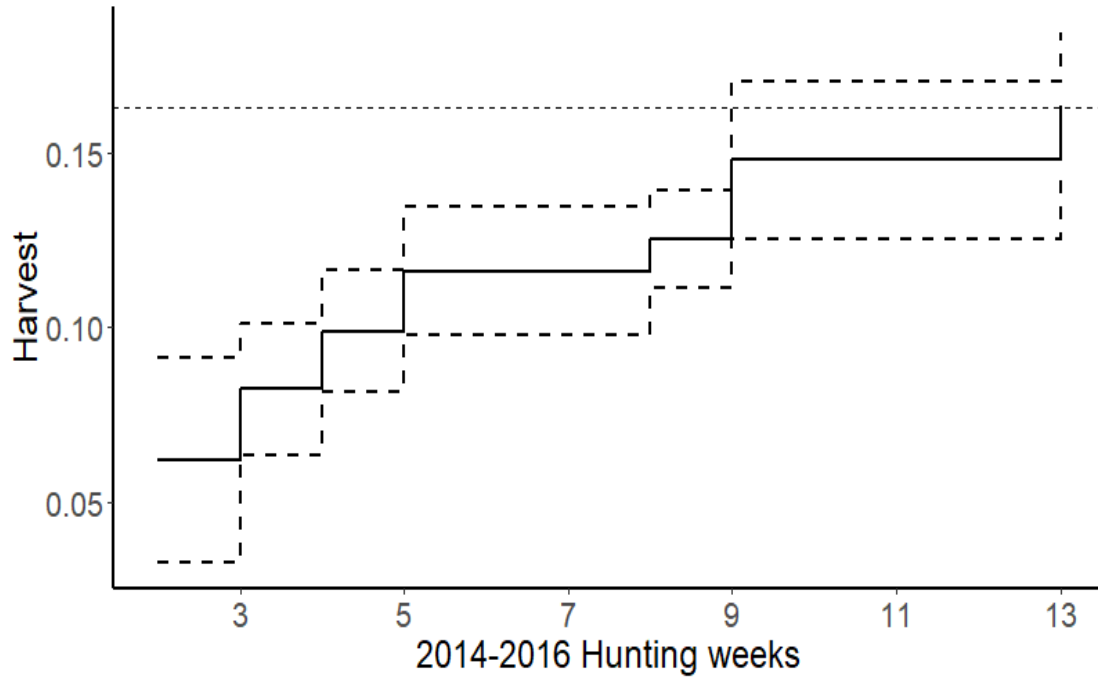


Figure 4. Weekly cumulative harvest rates of radio-marked ruffed grouse in central Maine from October through December, 2014-2016, pooled across all years and study areas. Dashed lines represent the upper and lower limits of 95% confidence intervals. The cumulative annual harvest rate across three years is indicated by the horizontal dotted line.

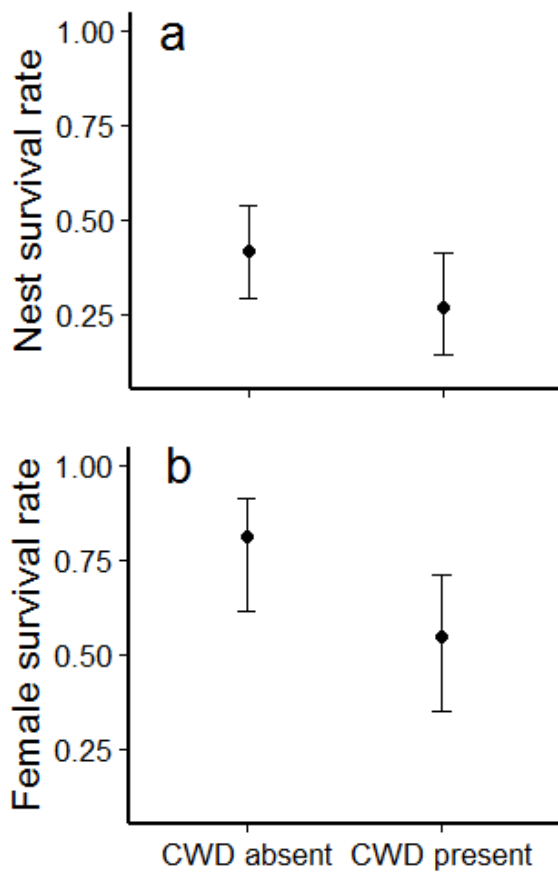


Figure 5. Effects of Coarse Woody Debris on nest survival and female survival while nesting. Model selection results showed that CWD (Coarse Woody Debris; dead woody vegetation  $\geq 10\text{cm dbh}$ ) decreased (a) the probability of nest survival and (b) the probability of female survival while nesting for ruffed grouse at two study areas in central Maine, USA, during springs 2015-2017. Gray ribbons represent 85% CIs of the modeled relationships.

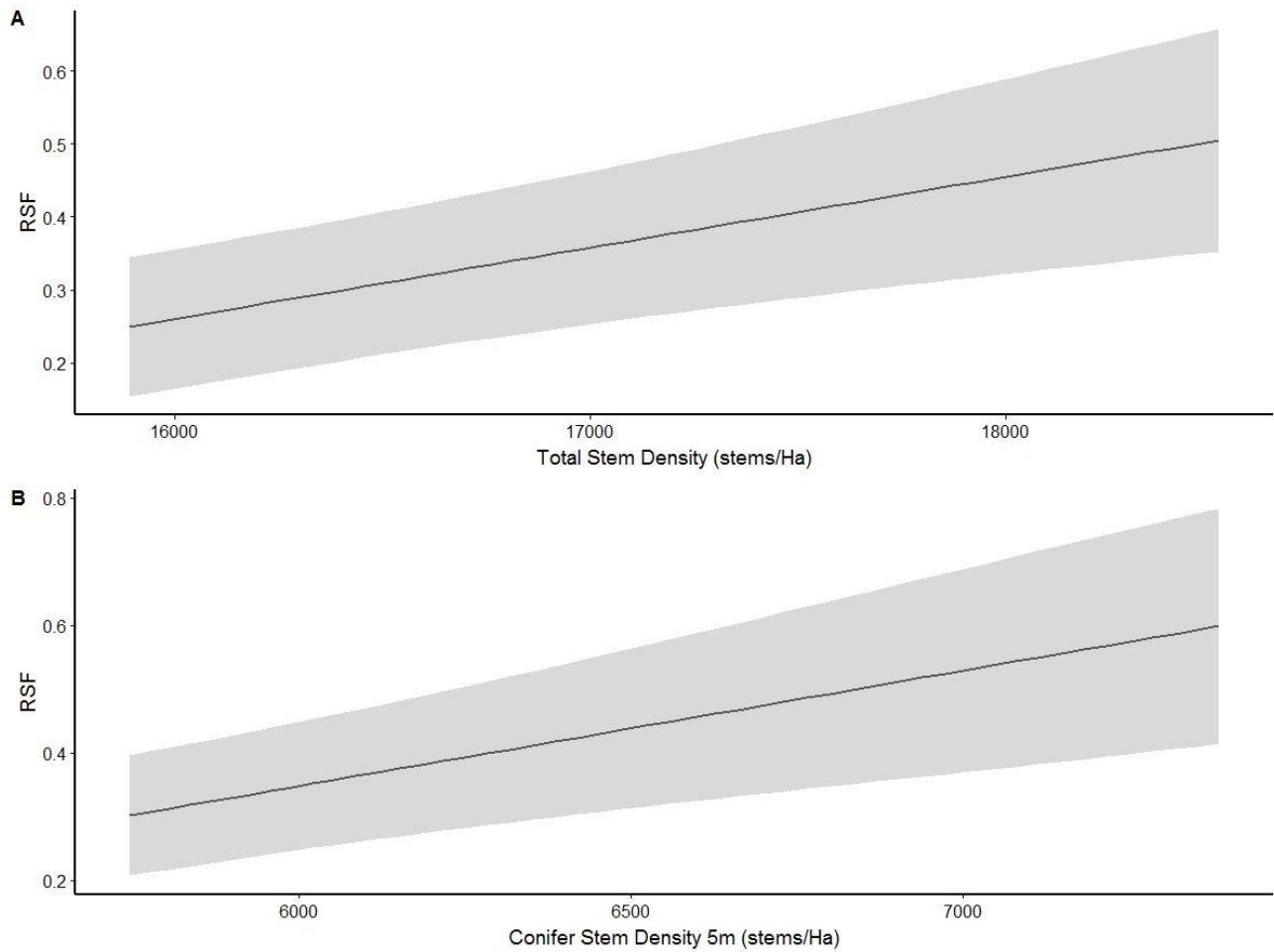


Figure 6. Selection of habitat characteristics by male ruffed grouse at display locations in two study area in central Maine, USA for spring 2015 and 2016. Ruffed grouse exhibited the greatest selection for A) woody stem density  $\leq$  10-cm dbh, and B) conifer stem density within 5m from display stages. Stem densities were quantified using a 30-m belt transect perpendicular to the stage. Shaded areas represent 95% confidence intervals.

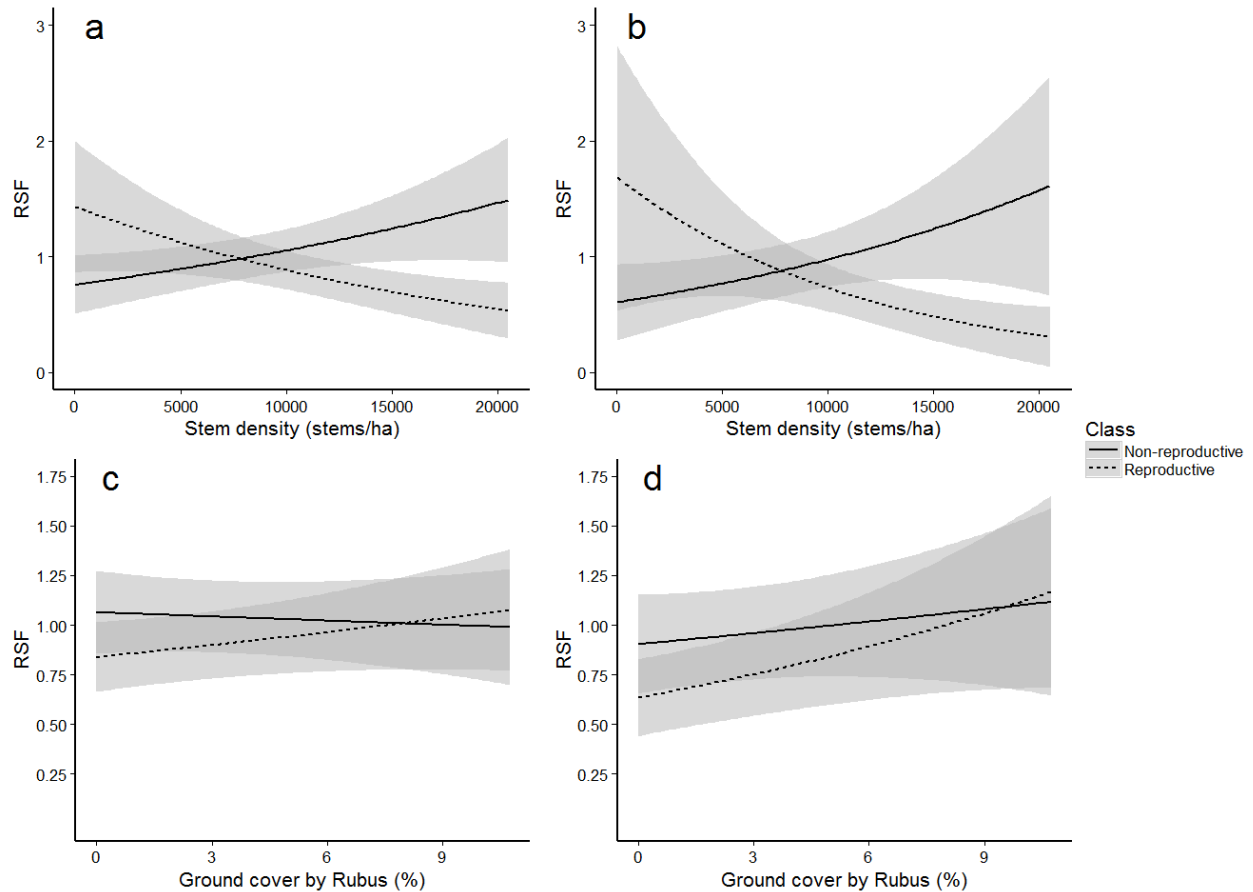


Figure 7. Resource selection functions for stem density and ground cover by *Rubus*. Resource selection functions (RSFs) are for brood-rearing and non-reproductive ruffed grouse at two study areas in central Maine, USA, June through mid-August 2015 and 2016. a) Relative selection of woody stem density compared to landscape-level resource availability. b) Relative selection of woody stem density compared to local-level resource availability (50-200-m from used points). c) Relative selection of ground coverage by *Rubus* compared to landscape-level resource availability. d) Relative selection ground coverage by *Rubus* compared to local-level resource availability, gray ribbons represent 85% CIs.

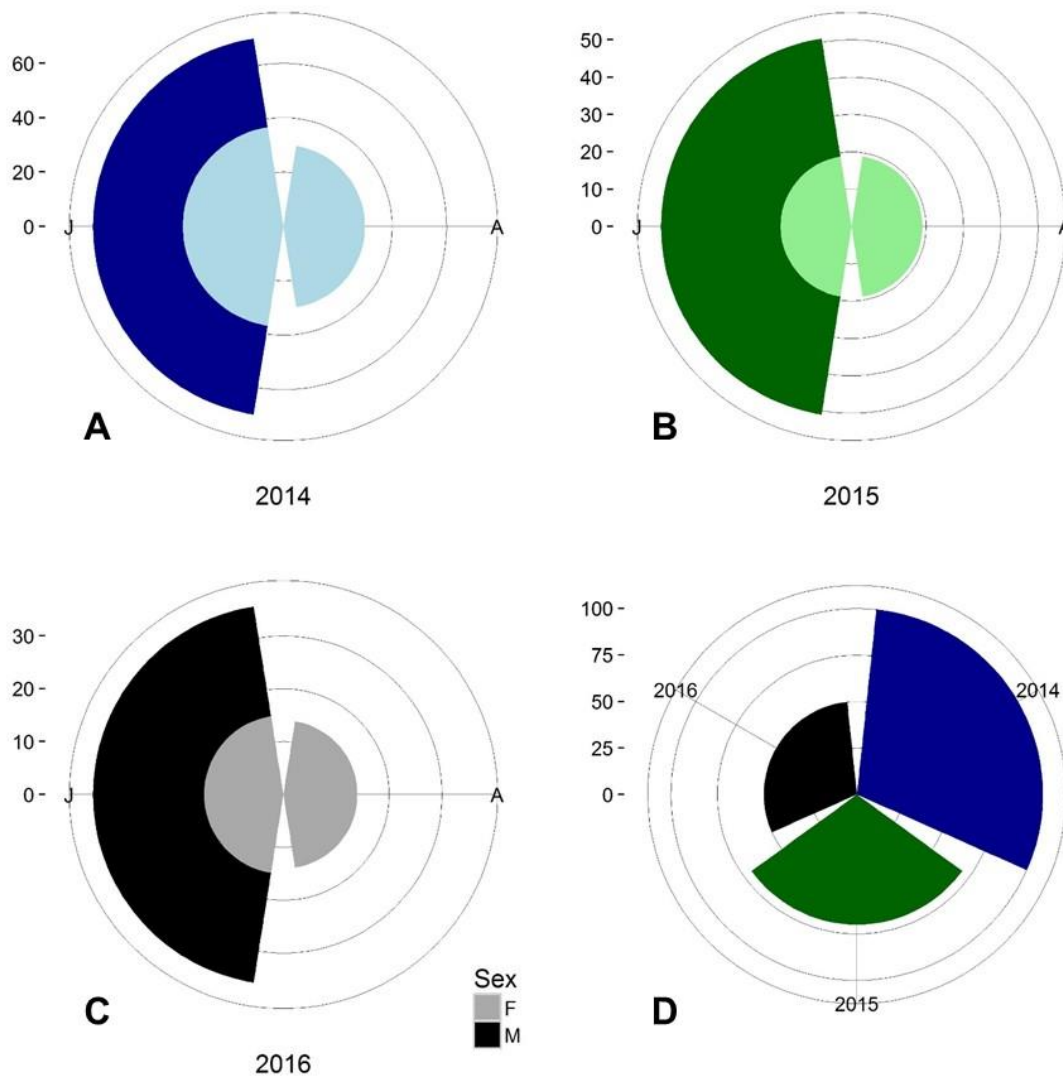


Figure 8. Visual depiction of the variation in age ratios (juveniles to adult females) for ruffed grouse captured during 2014 (A), 2015 (B), and 2016 (C) at two study areas in central Maine, USA. The total number of individuals captured (D) varied substantially among the three study years. In panels A, B, and C, the lighter shade reflects female birds, with adults shown on the right half of each figure, while the darker shade reflects juvenile male birds.

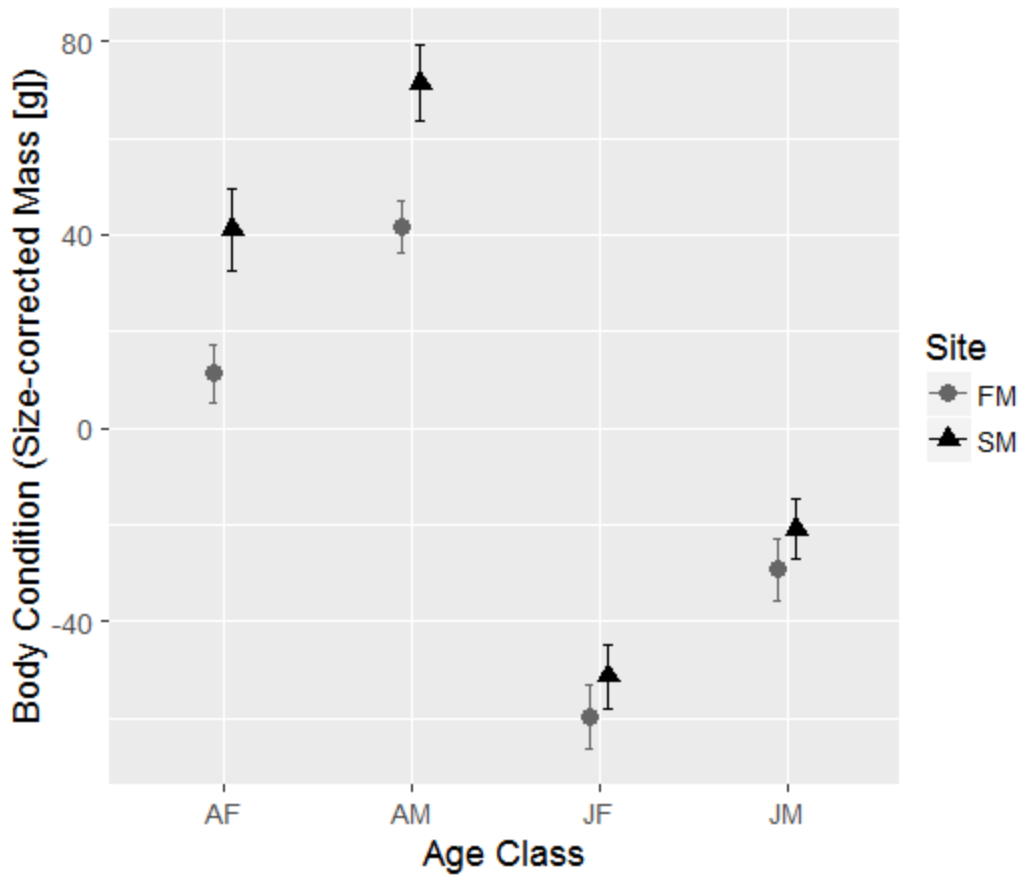


Figure 9. Variation in ruffed grouse body condition (body mass (g) adjusted for structural size) among age/sex classes and study areas (sites; FM = Frye Mountain, SM = Stud Mill). Estimates are based on a generalized linear model that included additive effects of age, sex, site, and date of capture, as well as an interaction between age and site. Data are from birds captured during August and September, 2014-2016, and include only newly-captured individuals (N=313). AF = Adult Female, AM = Adult Male, JF = Juvenile Female, JM = Juvenile Male.

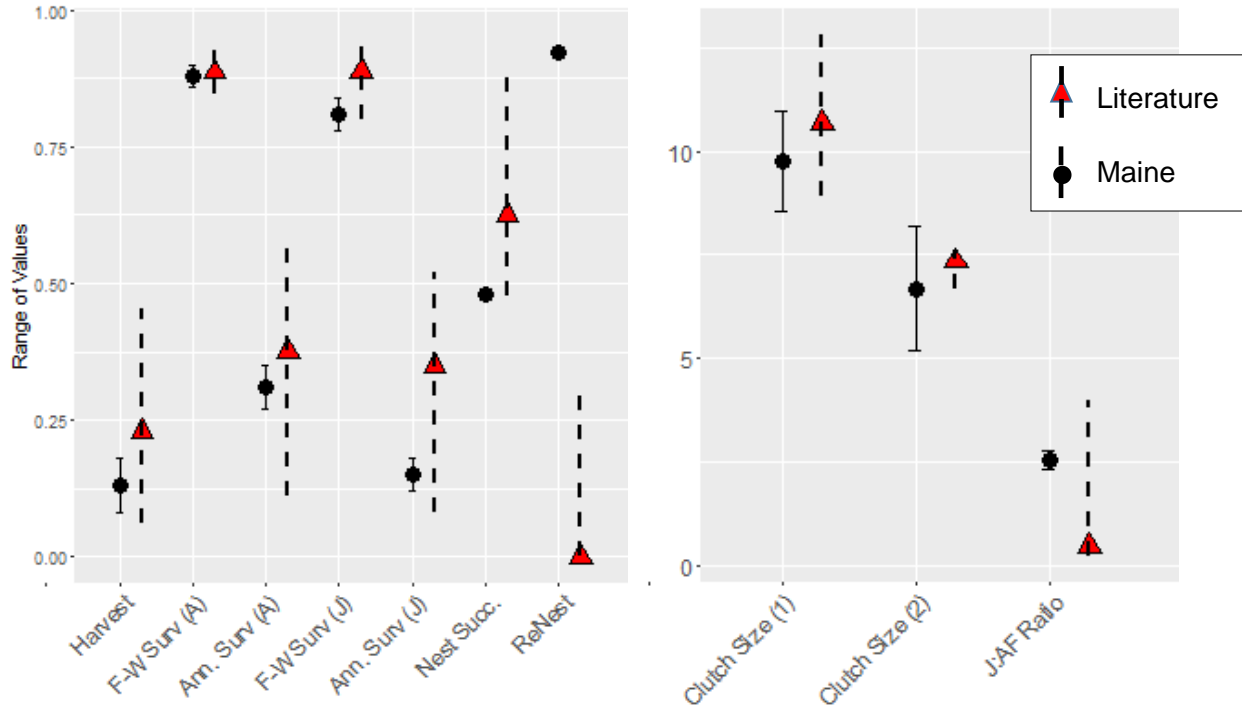


Figure 10. Demographic estimates for Maine ruffed grouse from this study (solid black circles, error bars = SE) compared with the median (red triangles) and range of values (dashed black lines) reported in the literature. Citations for literature sources are given in Table 13.

## **APPENDIX 1 – PROJECT COMMUNICATION PRODUCTS TO DATE**

### *Public Outreach Activities*

1. Presented project results to a combined meeting of the Penobscot County Chapter of the Maine Woodlot Owners Association and Hirundo Wildlife Refuge. Old Town, Maine, March 2017.
2. Presented project results at the Maine Woodlot Owners Association annual conference, Augusta, Maine, January 2017
3. Gave an update on our research at the Central Maine Chapter of the Ruffed Grouse Society Annual Banquet in Brewer, Maine, November 2016.
4. Gave an informal talk on our research and grouse ecology during winter to a group of 9-12<sup>th</sup> graders at Old Town High School. October 2016.
5. Presented a talk entitled “Wildlife, winter, and the ecology of ruffed grouse” and gave a radio-telemetry demonstration to a group of approximately 40 3<sup>rd</sup>, 4<sup>th</sup>, and 5<sup>th</sup> grade students at Appleton Elementary School, Appleton, ME. January 2016.
6. Presented a talk on our research and grouse ecology during winter to the Acadia Learning Snowpack Project members – a group of K-12 educators that integrate winter ecology into their classrooms. February 2015.
7. Delivered an invited talk in the Merryspring Nature Center Weekly Lecture Series titled “Ruffed Grouse Ecology, Conservation, and Research in Maine”. Merryspring Nature Center, Camden, Maine. January 2016.
8. Gave an informal talk on our research and grouse ecology during winter, and worked with 9<sup>th</sup>-12<sup>th</sup> grade students at Old Town High School to set up snow survey transects. January 2015.
9. Gave an update on our ongoing ruffed grouse research at the Central Maine Chapter of the Ruffed Grouse Society Annual Banquet in Brewer, Maine, November 2015.



10. Presented a talk titled: “Ruffed grouse ecology, research, conservation, and hunting in Maine” to the Falmouth Rod and Gun Club, Falmouth Maine, November 2014.

### *Press Coverage*

1. Our research was profiled as an article in the Fall 2015 issue of Bangor Metro Magazine. September 2015.
2. Samantha Davis was interviewed and our ruffed grouse project was highlighted on the weekly radio program “The Maine Birding Trail” with Bob Duchene. May 2014.
3. E. Blomberg and B. Allen appeared on the Maine Outdoors Radio Show to discuss the project. August 2014.
4. Our research was highlighted in three articles written by B. Allen in the Northwoods Sporting Journal; May and June 2014; September 2016.
5. E. Blomberg and K. Sullivan were interviewed, and our research project was highlighted, on the front page of the Bangor Daily News Outdoors Section. A 3-minute video starring K. Sullivan was produced by BDN and published on their web page. September 2014.
6. E. Blomberg was interviewed about our research by the Maine Public Broadcasting Network. That interview was aired on MPBN Radio and was highlighted on their website.

### *Technical Reports*

1. Davis, S., J. Mangelinckx, and E. Blomberg. 2017. Understanding population ecology of ruffed grouse inhabiting multiple use forest landscapes to inform habitat and harvest management. Final Progress Report. 68 pgs.
2. Mangelinckx, J., M. E. Martin, and E. J. Blomberg. 2017. Monitoring population dynamics of Maine ruffed grouse using spring drumming surveys. Year 4 Progress Report. 33 pgs.

3. Davis, S., J. Mangelinckx, and E. Blomberg. 2016. Understanding population ecology of ruffed grouse inhabiting multiple use forest landscapes to inform habitat and harvest management. Year 2 Progress Report. 56 pgs.
4. Mangelinckx, J., S. Davis, and E. Blomberg. 2015. Understanding population ecology of ruffed grouse inhabiting multiple use forest landscapes to inform habitat and harvest management. Year 1 Progress Report. 38 pgs.
5. Blomberg, E. J., and M. E. Martin. 2015. Monitoring population dynamics of Maine ruffed grouse using spring drumming surveys. Year 2 Progress Report. 25 pgs.
6. Martin, M. E., and E. J. Blomberg. 2014. A first year assessment of ruffed grouse drumming survey protocols in Maine. Year 1 Progress Report. 14 pgs.

#### *Professional Presentations*

1. Mangelinckx, J. Reduced female survival during reproduction in a ground-nesting bird. British Ornithologists' Union Twitter Conference. Nov. 2017. Online Conference.
2. Blomberg, E. J. Two birds, one stone: bringing basic perspectives to applied research on eastern game birds. University of New Hampshire Environmental Sciences Seminar Series. November 2017.
3. Blomberg, E.J., S. Davis, J. Mangelinckx, K. Sullivan, R. B. Allen. A full annual perspective on ruffed grouse survival in Maine. Northeastern Upland Game Bird Technical Committee Fall Meeting. Winter Harbor, ME. September 2017.
4. Mangelinckx, J. Nesting ecology and summertime resource selection of ruffed grouse in central Maine, USA. Department of Wildlife, Fisheries, and Conservation Biology, Orono, ME. July 2017. Thesis Defense.
5. Davis, S. R. Survival, Harvest, and Drumming Ecology of Ruffed Grouse in Central Maine USA. Department of Wildlife, Fisheries, and Conservation Biology, Orono, ME. June 2017. Thesis Defense.

6. Mangelinckx, J., S. Davis, R. B. Allen, K. Sullivan, and E. J. Blomberg. Ruffed Grouse Population Ecology in Maine Forests. Wagner Forestry Management Training Session, West Forks, ME. May 2017. Oral Presentation.
7. Mangelinckx, J., S. Davis, R. B. Allen, K. Sullivan, and E. J. Blomberg. Reproductive status affects summertime resource selection and survival of Ruffed Grouse in Maine. UMaine Student Research Symposium, Bangor, ME. April 2017. Oral Presentation.
8. Davis, S. R., J. Mangelinckx, B. Allen, K. Sullivan, and E. J. Blomberg. Survival and Harvest of Ruffed Grouse in Central Maine, USA. UMaine Student Research Symposium, Bangor, ME. April 2017. Oral Presentation.
9. Davis, S. R., E. J. Blomberg, J. Mangelinckx, B. Allen, and K. Sullivan. Drumming Ecology of Male Ruffed Grouse in Central Maine, USA. Maine Cooperative Fish and Wildlife Research Unit Annual Meeting, Orono, ME. March 2017. Poster.
10. Mangelinckx, J., E. J. Blomberg, S. Davis, R. B. Allen, and K. Sullivan. Summer Habitat Selection by Non-Reproductive Ruffed Grouse in Maine. Maine Cooperative Fish and Wildlife Research Unit Annual Meeting, Orono, ME. March 2017. Poster.
11. Sullivan, K., E.J. Blomberg, M. Martin, and A. Demusz. Spatial and Temporal Trends in Density and Site-Occupancy of Ruffed Grouse in Maine. The Wildlife Society Annual Conference, Raleigh, NC. October 2016. Poster
12. Mangelinckx, J., E.J. Blomberg, S. Davis, B. Allen, and K. Sullivan. Summer Habitat Selection by Non-Reproductive Ruffed Grouse in Maine. The Wildlife Society Annual Conference, Raleigh, NC. October 2016. Poster
13. Davis, S., E.J Blomberg, J. Mangelinkx, B. Allen, and K. Sullivan. Seasonal Survival and Harvest Rates of Ruffed Grouse in Central Maine, USA. The Wildlife Society Annual Conference, Raleigh, NC. October 2016. Poster
14. Mangelinckx, J., E.J. Blomberg, S.B. Davis, B. Allen, and K. Sullivan. Nest-Site Selection and Nesting Success of Ruffed Grouse in Maine. The Wildlife Society Annual Conference, Raleigh, NC. October 2016. Poster

15. Davis, S., E.J Blomberg, J. Mangelinckx, B. Allen, and K. Sullivan. Habitat Selection and the Effects on Male Ruffed Grouse Display Behavior and Performance in Central Maine, USA. The Wildlife Society Annual Conference, Raleigh, NC. October 2016. Poster
16. Blomberg, E. J. Occupancy Analysis and its Application to Bat Population Monitoring. Paper. International Bat Research Symposium, Winter Harbor, ME, April 2016. The Wildlife Society Annual Conference, Raleigh, NC. October 2016.
17. Davis, S., E. J. Blomberg, J. Mangelinckx, R. B. Allen, and K. Sullivan. Harvest, Seasonal Survival, and Drumming Ecology of Ruffed Grouse in Maine, USA. Poster. Maine Cooperative Fish and Wildlife Research Unit Annual Meeting. Orono, ME, March 2016.
18. Mangelinckx, J., E. J. Blomberg, S. Davis, R. B. Allen, and K. Sullivan. Nest-site selection and nest success of ruffed grouse in Maine. Poster. Maine Cooperative Fish and Wildlife Research Unit Annual Meeting. Orono, ME, March 2016.

#### *Graduate Theses*

1. Davis, S. 2017. Survival, harvest, and drumming ecology of ruffed grouse in central Maine, USA. M.S. Thesis, University of Maine.
2. Mangelinckx, J. 2017. Nesting ecology and summertime resource selection of ruffed grouse in central Maine, USA. M. S. Thesis, University of Maine

#### *Manuscripts submitted for publication*

1. Blomberg, E. J., S. Davis, J. Mangelinckx, and K. Sullivan. *In Press*. Detecting capture-related mortality in radio-marked birds following release. *Avian Conservation and Ecology*.
2. Davis, S., J. Mangelinckx, R. B. Allen, S. Sullivan, and E. J. Blomberg. *In revision*. Survival and harvest of ruffed grouse in central Maine, USA. *Journal of Wildlife Management*.
3. Mangelinckx, J., S. Davis, R. B. Allen, S. Sullivan, and E. J. Blomberg. *In review*. Reproductive status affects summertime resource selection and survival of Ruffed Grouse in Maine, USA. *The Auk: Ornithological Advances*.