Final Project Report: Population dynamics of spruce grouse in the managed forest landscapes of northern Maine.

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Plate 1. Images of a female spruce grouse (left) fitted with a radio transmitter, and an unmarked male spruce grouse (right).

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PROJECT SUMMARY

1. Spruce grouse (*Falcipennis canadensis*) are a non-migratory obligate resident of conifer forests throughout northern North America. The species reaches the southeastern extent of its distribution in the northeastern U.S. where it is considered a species of concern. Spruce grouse occur throughout Maine, often in forests used extensively for commercial forestry.

2. We studied demographics of spruce grouse from 2012 through 2018 in an area comprised primarily of commercially-managed forest in north-central Maine, which is commonly referred to as the Telos region. We used radio telemetry to locate nests, monitor broods, and detect mortality of both juvenile (post-independence but prior to first breeding) and adult (post-first-breeding) spruce grouse.

3. We evaluated the consequences of spruce grouse use of forest stands with varying management histories (silvicultural treatments and time since stand harvest) on nest success, brood success, juvenile survival, and adult survival. We also constructed stage-structured population models to: a) quantify spruce grouse population growth rates based on our measured demographic rates; b) evaluate potential vital rate contributions to population growth; and c) illustrate the potential contributions of forest management to population growth.

4. We monitored survival of 43 juvenile and 116 adult radio-marked spruce grouse during our 6-year study, and located and monitored 26 nests and 60 broods. We collected >1000 spruce grouse locations that contributed to our understanding of spruce grouse use of commercial forest stands.

5. The effect of forest stand characteristics was diverse and depended on life stage. In general, stand treatment type (clearcut, clearcut with post-harvest herbicide and thinning, or residual stands unharvested since at least 1982) was a better predictor of spruce grouse demographics than time since stand harvest. Nests located in clearcuts with post-harvest treatment had lower success than all other stand types. Survival of broods during summer increased with more proportional use of residual stands; however juvenile spruce grouse that made greater use of residual stands during their first fall and winter had reduced survival. Adults that used a higher proportion of clearcuts without post-harvest treatment had the greatest annual survival.

6. Mean vital rates from our study predicted a declining population, with both deterministic (λ_D=0.714) and stochastic (λ_S = 0.680; 95% CI = 0.588 to 0.771) models predicting values of λ<1.0. Based on annual estimates of all vital rates, positive growth (λ>1.0) was observed during 1 of 6 study years. We found that adult survival had the greatest potential to influence population growth, and accordingly, greater use of untreated clearcuts by adult birds had the greatest potential to increase population growth.

7. Spruce grouse exhibited demographic rates during our 6-year study that were consistent with population decline. Ours represents one of the most comprehensive demographic studies of the species to date; however, we may have not captured the full range of annual variation in this system. Nevertheless, our results suggest future decline of this population and the need for additional long-term monitoring and assessment of Maine's spruce grouse.

INTRODUCTION

Spruce grouse (*Falcipennis canadensis;* Plate 1) are native birds that inhabit conifer forests throughout the northern U.S. and Canada (Allan 1985, Schroeder et al. 2018). The species is typically associated with forests dominated by short-needled conifers such as spruces (*Picea* spp.), firs (*Abies* spp.), jack pine (*Pinus banksiana*), and tamarack (*Larix laricina*), and this close association results in part from digestive adaptations that allow spruce grouse to persist for much of the year on a diet comprised of the needles of conifer trees. The Acadian forest region throughout northern Maine provides such habitat to spruce grouse, primarily in the form of lowland and upland stands dominated by balsam fir (*A. balsamea*), spruce, and tamarack. Many of these forests are intensively managed for commercial forest products.

Throughout the northeastern US spruce grouse are considered to be of conservation concern. New York and Vermont currently list spruce grouse as a state endangered species (Ross and Johnson 2012, Alexander and Parren 2012), and in New Hampshire spruce grouse are considered a species of conservation concern (Perry 2005). In Bird Conservation Region (BCR) 14, which includes Maine, the Spruce Grouse Continental Conservation Plan states that spruce grouse populations are fragmented and vulnerable to extirpation in the southeastern portion of the BCR, whereas more northern populations in Canada are considered secure (Perry 2005). Spruce grouse occur throughout northern Maine, and they are listed in the Maine Wildlife Action Plan as a category 3 species of greatest conservation need. However, relatively little work has been done to assess their current population status in the state.

Maine's Acadian forest rests along the transition zone between the conifer-dominated boreal forests to the north, where spruce grouse are generally considered widespread and abundant, and the hardwood-dominated eastern deciduous forests to the south, where potential habitat for spruce grouse becomes increasingly limited (Schroeder et al. 2018). Spruce grouse populations are likely sensitive to habitat alteration and reduction in extent of conifer stands along their southern range boundary (Schroeder et al. 2018). The Acadian forest may represent an important transition zone between northern and southern populations, and intensive management of conifer stands within Maine's forest landscapes are likely to have a strong influence on the state's spruce grouse populations. In fact, recent assessments indicate a reduction in conifer forest and an associated increase in deciduous-dominated and mixed conifer-deciduous forests over the past several decades in northern Maine (Legaard et al. 2015), which suggests that habitat for spruce grouse may be declining in that region.

Intensive forestry is often hypothesized to reduce the diversity and abundance of wildlife, particularly for species associated with mid- and late-successional conifer forests. In many portions of the species' range, however, spruce grouse are found in high densities in early- and mid-successional conifer forests that are maintained by disturbance such as fire (Schroeder et al. 2018). The extent to which timber harvesting in Maine's commercially managed conifer forests promotes habitat conditions that are favorable to spruce grouse persistence is currently unclear. Working in the Telos region of northern Maine, Dunham (2016) estimated stand occupancy and abundance of male spruce grouse in a variety of forest stand types, and confirmed that spruce grouse make extensive use of managed conifer stands, in particular those that received significant

post-harvest treatments in the form of thinning and herbicide application to control deciduous growth. This suggested that commercial forestry may promote structural characteristics consistent with spruce grouse habitat requirements (Schroeder et al. 2018). Importantly, however, resource requirements of male spruce grouse during the breeding season may differ dramatically from those of females, who provide sole parental care and are the sex responsible for population maintenance. Thus, habitat conditions associated with high occupancy or abundance of males may not be synonymous with features that promote population growth or stability, and there remains a need to understand how forest practices affect the individual vital rates (e.g., brood survival, juvenile survival, survival of adult females) that affect the population status of spruce grouse.

We approached this project with the goal of evaluating spruce grouse population ecology in the commercially-managed forests of northern Maine. Doing so would allow us to both evaluate the current population trajectory of spruce grouse in a region that is representative of Maine's northern conifer forest, and to assess the contributions of forest management practices on spruce grouse demographic rates. Our specific objectives were as follows:

Objective 1: Estimate demographic rates of spruce grouse using a combination of radio-telemetry and capture-mark-recapture methods. Monitor within a range of different forest management treatments and varying habitat composition.

Objective 2: Evaluate forest stand characteristics at locations used by spruce grouse during important life phases (e.g. brood rearing or nesting) and determine the influence of stand management treatments on demographic rates.

Objective 3: Relate objectives 1 and 2 to population performance using predictive stage-structured population models. Use these models to evaluate the overall trajectory of spruce grouse populations, and classify populations as stable, increasing, or experiencing decline.

Objective 4: Provide guidance in the form of a status evaluation and recommendations for future conservation of spruce grouse populations, to include evaluation of forest management activities that promote forest stand conditions that are consistent with healthy spruce grouse populations.

To address these objectives, we used radio telemetry to collect detailed demographic data on spruce grouse in the Telos region of northern Maine during a 6-year study period that extended from 2012 to 2018. We evaluated spruce grouse use of conifer stands with varying management approaches and harvest histories, and quantified nest success, brood success, survival of juvenile birds to first breeding, and adult survival. We then related stand use to each of these demographic rates, used stage-structured population models to evaluate population growth rate, and evaluated the relative potential for each stand management type to influence population growth.

STUDY AREA

Our primary study area was the Telos region located in in Piscataquis County, northern Maine (Figure 1). This region was almost exclusively forested, with the only

non-forest landcover comprised of water bodies (lakes and rivers) or open water wetlands. Deciduous-dominated forest stands were comprised of American beech (*Fagus grandifolia*), maple (*Acer* spp.), birch (*Betula* spp.), aspen (*Populus* spp.), and other deciduous species, while conifer-dominated stands were typically dominated by spruces and balsam fir, with lower densities of white pine (*Pinus strobus*), white cedar (*Thuja occidentalis*), tamarack, and hemlock (*Tsuga canadensis*). Mixed stands, which contained a combination of all of these trees, were also common. The primary land use in our study area was commercial silviculture to produce forest products; recreational use for hunting, fishing and other forms of outdoor recreation was also common. The entire region is comprised of second growth forest, with initial harvest occurring during the settlement of Maine during the late 1800s to 1940's. During the 1970s, a periodic outbreak of spruce budworm (*Choristoneura fumiferana*) was associated with large-scale clear cutting of spruce and fir throughout the region. Subsequently, many stands were managed to promote conifer-dominated regeneration through a combination of aerial herbicide application to suppress deciduous regrowth, and pre-commercial thinning of conifer stems. The majority (~80%) of our study area was privately owned and managed by several large private landowners and land management companies. Our study area also included portions of the Scientific Forest Management Area of Baxter State Park, and a few small-scale private inholdings.

METHODS

The project period associated with this report (2014-2018; hereafter Phase 2), followed an earlier field study by The University of Maine in this area that occurred from 2012-2014 (hereafter Phase 1). Phase 1 focused largely on spruce grouse habitat use and

occupancy of managed forest stands (Dunham 2016), while during Phase 2 we placed

greater emphasis on Spruce Grouse demographics. This report incorporates more than

6 years of demographic data collected during both project phases. Where relevant, we

describe differences in methods between the two phases.
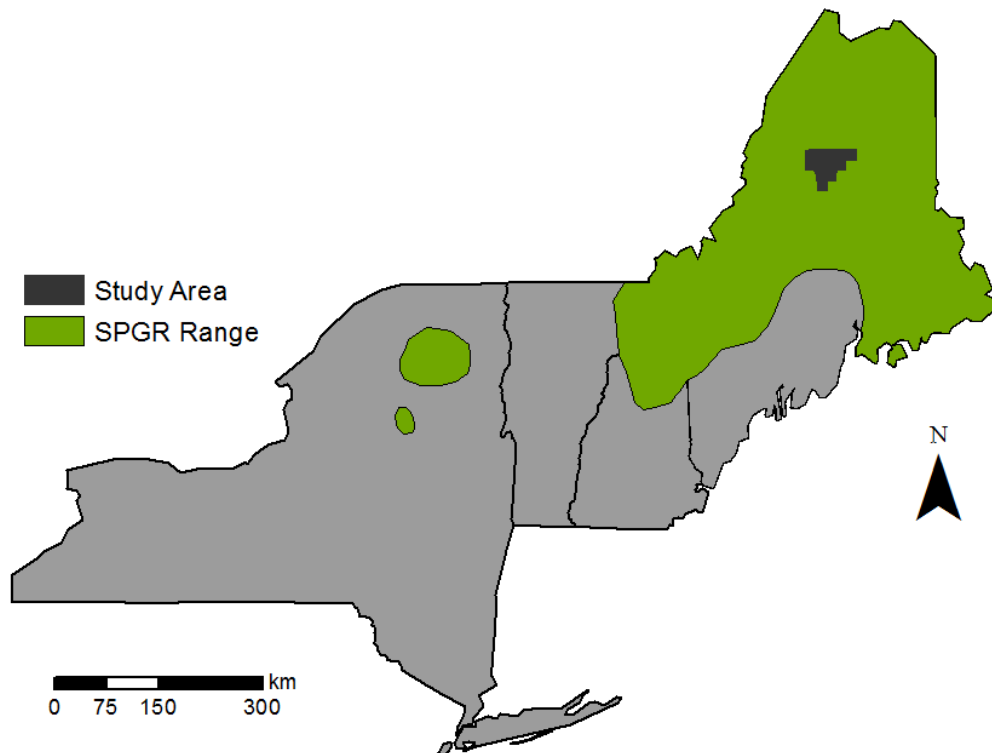
Figure 1. Location of study area in the Telos region of northern Maine, relative to the geographic distribution of spruce grouse within the northeastern U.S. We defined the study area on this map based on all townships in which we monitored spruce grouse.

Field Methods

   We captured male and female spruce grouse throughout the year using noose poles.

We located birds for capture using a variety of methods, including systematic surveys of

potential habitat aided by call playbacks of female cantus (territorial) calls and chick

distress calls (Dunham 2016), opportunistically while conducting other work, and by targeting individuals on roadsides while driving the extensive network of secondary forest roads within the system. All captured spruce grouse were individually marked using an aluminum leg band, and most birds were also fit with a necklace-style radio transmitter. Transmitters (Model A3950, Advanced Telemetry Systems, Isanti, MN) weighed 11 grams and featured a motion-sensitive switch that changed the signal pulse rate following 8 hours of inactivity, which allowed us to detect mortality remotely. We used our radio-marked sample of birds to collect data on nesting, brood-rearing, and individual survival as described below. Each time a marked individual was located, as well as at capture, we recorded the individual's location using a handheld GPS unit. All spruce grouse capture and handling was conducted under protocols approved by the University of Maine Institutional Animal Care and Use Committee.

Nesting

During the nesting season (approximately early May through late June) we located radio-marked female spruce grouse twice weekly by homing to their locations using a handheld radio receiver and antenna, and visually observed the female to document nesting status. When initially locating a female on a ne, we flushed her from the nest once to obtain a count of eggs (clutch size) and to determine incubation staging using the egg floating method (McNew et al. 2009). After discovery we monitored nests twice weekly without disturbing the female until she left the nest, at which point we determined nest fate based on egg shell remains and presence of chicks with the female. Nests were classified as either hatched (egg membranes detached from shell and chicks present with female) or failed (eggs crushed or missing, no chicks present).

Formal nest monitoring was not conducted during phase 1, so our dataset to evaluate nest success is restricted to nests discovered from 2015 through 2018.

Brood-rearing

We monitored broods associated with radio-marked females at least once weekly. For females with known nest locations, brood monitoring began one week following hatch and continued throughout the summer. Because we captured a large number of females already with broods using chick distress calls, not all broods came from known nests with established brood ages. In these cases, brood monitoring began following initial capture of the brood. Our methods for brood monitoring differed among phases of the study because of shifting project objectives. During Phase 1, a major objective was estimating home range size of females during the brood-rearing period, and so we collected frequent locations (e.g. daily) until at least 30 locations were obtained for each female. During Phase 2, we located broods less frequently, but attempted to do so at least once each week following hatch/capture through the end of the summer. During both phases, brood monitoring generally extended through mid to late August. Each time a brood was located, we determined brood status as active (chicks observed) or inactive. If chicks were observed, we also recorded a count of all chicks present and visible.

Individual survival and mortality

We monitored all individuals for live/dead status using a combination of radio signals and direct observations, but the frequency of monitoring varied among study phases and within years. Our most frequent monitoring occurred during our primary field

season (May through October), with less frequent monitoring during the off-season (November through April). During the primary field season we typically obtained information on the live/dead status of birds at least once per week, with much of this data coming from direct visual observations of birds. During 2016 and 2017 we employed additional field personnel during September and October to increase fall captures and to collect more frequent locations. During winter and early spring, we used a combination of periodic visits to the field site (aided by snowmobiles during winter) and fixed wing aircraft to monitor live/dead status. Occasionally we obtained location data during this period, but more typically we relied solely on "alive" or "dead" status of birds based on pulse rates of transmitters from radio signals.

Data Analysis

Stand Harvest Histories

For the purpose of this report, habitats were characterized (Objective 2) based on harvest type and history, as well as the post-harvest treatments (herbicide or PCT) applied after harvesting within forest stands used by spruce grouse. We obtained GIS layers of forest stand polygons from land managers that identified the year of timber harvest, type of harvest (e.g. clearcut, shelterwood), and any post-harvest treatments (herbicide application, PCT) that occurred within each stand. The spatial coverage of layers available to us included the vast majority (>90%) of our spruce grouse location data, and temporal coverage included the period from 1982 to 2017. We classified forest stands that occurred within the spatial extent of these GIS layers. Because no classification of "residual stands" was provided by landowners, for our purposes we considered a stand as "residual" if it did not have a harvest or post-harvest treatment

since at least 1981. We lacked information to determine the age or legacy of harvests occurring prior to 1981. Because it is likely that some of these stands were included in clearcutting that occurred during the 1970s, they do not represent mature forests, per se, but rather they reflect later succession second growth conifer forests distinct from the stands with more recent histories of harvest.

We intersected individual spruce grouse locations with forest stand layers to identify both time since harvest (hereafter 'stand age') and silvicultural treatment type (hereafter 'treatment type') for each location. Because we lacked specific information on the oldest stand ages, we could not rely on a continuous measure of stand age, and instead we aggregated stand age information into forest stages associated with general successional patterns within this system. These included 0 to 20 years post-harvest (sapling stage), 21 to 30 years (pole stage), and 31 years plus (tree stage). Because our spruce grouse location data were collected across a range of years, we assigned stand age based on the year of data collection. For treatment type, we initially considered 5 distinct categories (summarized in Table 1), however we further aggregated these types into 3 categories based on the relative distribution of spruce grouse locations within each stand type. We elected to aggregate the two categories with post-harvest treatments (thinning and thinning + herbicide) because we found relatively little spruce grouse use of sites that were only thinned without first receiving herbicide application, and these stand types were generally uncommon in the study area. Thus, this category became an aggregate that included all stands that were clearcut followed by a post-harvest treatment (hereafter 'Treated Clearcut'). Despite that partial harvesting was the dominant forest management treatment on our site from

1991 to 2016, we also found relatively little use by spruce grouse of stands harvested with partial overstory removal; presumably because this suite of silvicultural practices tend to promote greater deciduous regrowth which spruce grouse generally avoid (Schroeder et al. 2018). In this case, we decided to exclude this stand type from the analysis because of insufficient observations of use for evaluating effects on demographic rates,

Table 1. Description of 5 treatment types used to classify silvicultural history of conifer-dominated forest stands used by spruce grouse in Piscatiquis County, Maine.

Treatment Type[a]	Description
Clearcut (untreated)	Nearly complete overstory removal (<6.75 m^2/ha residual basal area), but lacking any post-harvest treatment to promote conifer regeneration.
Clearcut + Thinning	Clearcut (as above), followed by pre-commercial thinning approximately 10-20 years post-harvest to increase growth rate to marketable size.
Clearcut + Herbicide + Thinning	Clearcut (as above), followed by aerial application of herbicide (e.g., glyphosate) to reduce completion from deciduous regeneration approximately 5-15 years post-harvest, which was then followed by pre-commercial thinning (as above)
Partial Overstory Removal	Includes a variety of silvicultural methods (e.g. shelterwood, individual tree selection, group selection) that result in residual basal area (>6.75 m^2/ha) and summer canopy closure typically > 25%post-harvest.
Residual	Forested stands that did not receive harvest or post-harvest treatment since at least 1981.

[a] For our final analysis, we aggregated Clearcut + Thinning and Clearcut + Herbicide + Thinning categories into a single 'Treated Clearcut' category, and we also dropped the Partial Overstory Removal category, due to low use of this type.

To classify relative use of each treatment type and stand age class by spruce grouse, we summarized the proportion of each individual's locations (including capture locations) that fell within a given stand category for a particular life phase (e.g. brood rearing, juvenile). Thus, the unit of measure became proportional use by each bird based on all location information that was available for it. The lone exception to this was for nests, where we used a single discrete value for use or non-use of each category for each nest. For each demographic analysis, we visually inspected distributions of stand-level covariates to ensure that sampling was relatively equal across stand treatments, age categories, and study years, to ensure that any apparent effects of stand use were not confounded with other factors (e.g., if one stand class was disproportionately sampling during a year with very good or very poor conditions). Also, for our analysis of brood success (described below), we only used data on use locations for females known to have active broods when classifying stand treatment type and age. This was necessary because female grouse may shift habitat use following brood loss; thus including forest stand use for females following brood loss could confound the process of stage-specific habitat selection with the effects of forest stand treatments on brood survival. In a small number of cases (<5%) we lacked any location data from individual spruce grouse to classify habitat use. We z-standardized (mean = 0.0, sd = 1.0) all covariate values and applied a value of 0.0 in the case of missing data. In this way birds that lacked stand use information still contributed to parameter (e.g. monthly survival rate) estimation (i.e. through the model intercept term) but did not influence covariate relationships (e.g., effects of forest harvest treatment on survival).

Demographic Analyses

We conducted all demographic analyses using the package RMark (Laake 2017) in Program R, which implements analyses in a maximum likelihood framework using the software Program MARK (White and Burnham 2002). We used nest survival analyses to quantify daily survival rates (DSR) of nests. We further calculated overall nest success for both the laying and incubation periods (Blomberg et al. 2015) as DSR^{32}, which accommodates an 8-day laying period and 24 days of incubation.

We also used nest survival analysis to evaluate the monthly survival probability of juvenile and adult spruce grouse. Nest survival analysis was well-suited for analyzing survival of our radio-marked birds because it does not assume a known timing of death, which is important when fates are determined at irregular intervals and, as such, may be poorly suited to other analytical approaches (Blomberg et al. 2013, Davis et al 2018). Juvenile survival was analyzed across an 8-month period from September, when broods typically disbanded, through the month of April, and we assumed that during May juveniles transitioned to adulthood coincident with their first potential nesting attempts. Survival of juveniles (S_J) was derived from the mean monthly survival probability raised to the 8th power, and represented the probability of individual survival from independence to first breeding. We conducted a separate analysis for adult survival, which was modelled for the entire calendar year, and where we calculated annual survival of adults (S_A) by raising the mean monthly survival probability to the 12th power. We computed estimates of SE for each derived estimate using the Delta Method (Powell 2007).

To quantify spruce grouse success during the brood-rearing period, we elected to focus on brood success, rather than survival of individual chicks, for two reasons. First, many of our brood-rearing females were initially captured with a brood after their eggs had hatched and they had left their nest, and thus we lacked data on initial brood sizes or the specific age of broods at first capture. Secondly, it was difficult to consistently obtain counts of chicks in the dense vegetation typical of their forested habitat. For these reasons, our repeated counts of chicks did not conform to assumptions for methods available to estimate survival of young from marked parents (Luckaks et al. 2004). Instead, we aggregated observations of brood status into a weekly brood survival history, and analyzed these data using a Cormack-Jolly-Seber (CJS) live encounter analysis (Sandercock 2006), which incorporates detection probability (p) to derive estimates of apparent survival probability (Φ). We defined our brood survival history based on the 12-week period from early-June until the end of August, which includes the period from our earliest brood observation until the beginning of juvenile independence. For each radio-marked female with a brood during each week of this season, we classified status as 1 for cases where we observed chicks, or 0 in cases where we either did not observe the female or failed to observe evidence of a brood. Under the CJS framework, Φ then gives the weekly probability that a female with a brood retained her brood (brood survival) and 1- Φ gives the probability of total brood loss. Under our construction of the survival history, p represented the probability that an active brood was not observed, either because we failed to detect chicks or because the female was not located during a particular week. From the weekly estimates of Φ, we derived the overall probability of brood success (BS) as $BS=\Phi^{10}$, where 10 weeks

represented the average length of time between the mean hatch date of nests and September 1.

Prior to testing stand-level variables, we first incorporated other sources of potential variation such as individual sex, year, and within-year temporal variation (e.g. weekly or monthly) as appropriate for each analysis. If any of these model structures were supported based on AIC_c (i.e. reduced AIC_c relative to an intercept-only null model), we retained them as a base model structure in further models to test effects of stand-level covariates. We then included each covariate describing proportional use of each stand age class or treatment type as an additional additive effect combined with the base model structure for each analysis. We evaluated support for stand covariates using AIC_c, where a value of ΔAIC_c <2.0 indicated model support. We further interpreted 85% confidence intervals of stand level covariate effects from supported models as a secondary check on whether covariates were informative (Arnold 2010). For each analysis, we explored the realized effect of supported stand-level covariates by comparing standardized beta coefficients and by visually inspecting prediction plots illustrating the slope of the covariate effect.

We also used and interpreted results of a Year model (i.e. study year as a fixed effect) in each analysis, regardless of AIC_c support for that model, to better-understand annual variation in spruce grouse vital rates during our study. These estimates were also used to implement stochastic population models (described below).

Population Model

We used the mean demographic estimates described above (nest success, brood success, juvenile survival, adult survival) to construct a deterministic model (Caswell 2001) of spruce grouse population dynamics. In addition to the model-derived estimated values, we quantified a number of additional demographic values from our data, and where necessary used values from the literature. These included nesting propensity (*NP*), clutch size for first (*CS1*) and second nests (*CS2*), egg hatching rate (*EH*), renesting probability (*RNP*), and chick survival (*ChS*). We found nests for all females that we followed with sufficient frequency during the nesting season, so we assumed that *NP*=1.0. We observed a small number of females that initiated a second nest in a single season (n=2), but generally we lacked data to estimate an unbiased probability of renesting directly (e.g. Blomberg et al. 2017), so, we used a conservative value of *RNP*=0.25*.* Mean clutch size during our study was *CS1*=5.87, and we assumed that second clutches would be 1 egg smaller (*CS2*=4.87). We assumed that egg failure (e.g. infertility) was relatively low, and set *EH*=0.90, and we also assumed an even primary sex ratio. Because our brood survival term accounted for rates of complete failure, *ChS* represented the proportion of chicks that remained in broods given that a brood was successful, which was given as

$$ChS = \frac{Brood\ Size_{10}}{CS * EH}$$

where we derived Brood Size$_{10}$ by taking the maximum of chick counts from all active broods during the last 2 weeks of August, and averaging this among all active broods.

We used the values described above to calculate fecundity, *F*, for each age class, generally following the equation developed by McNew et al. (2012) as:

$$F_i = [(NP_i NS_i CS1_i) + (NP_i(1 - NS_i)RNP_i NS_i CS2_i)] * BrS_i ChS_i EH_i * 0.5$$

which returned per-capita production of female chicks to independence for each age class (i), while accounting for contributions of both first and replacement nesting attempts.

We developed a two-stage projection matrix assuming a post-breeding census, which took the form:

$$M = \begin{bmatrix} F_J S_J & F_A S_A{}^{0.75} \\ S_J S_A{}^{0.25} & S_A \end{bmatrix}$$

Because we generally lacked age-specific values for most vital rates, we used the same values for fecundity (F) for each of the two age classes. Under the post-breeding census, the upper matrix elements include the stage-specific survival terms to accommodate loss of individuals prior to the onset of reproduction (Mills 2013, Kendall et al. 2019). Our approach to modelling nest success and brood success incorporated reproductive failure due to female death during nesting and brood-rearing, respectively. Therefore, it was only necessary for these survival terms to cover the 8-month period between brood breakup and the onset of nesting. In the case of juvenile survival, our estimated value of S_j was relative to the non-breeding period, so we needed to extend survival in the lower left matrix element to a full year, which we did using a 3-month

survival probability from the adult age class (given that juveniles transitioned to adulthood at first breeding).

We used the popbio package in Program R, which implements methods for stage-structured population modeling as described by Caswell (2001) and Morris and Doak (2002), to quantify characteristics of the projection matrix. We quantified the deterministic rate of population growth (λ_D) based on mean vital rates for the entire study period, and we also computed the stochastic growth rate (λ_S) which allowed us to characterize both the mean and 95% confidence intervals of the population projection. In the later case, we used vital rate matrices populated with estimates from each year of the study and simulated stochastic growth for a 25-year interval by randomly drawing values from each of the six annual matrices. We replicated the simulation 500 times, used the geometric mean of the replicates as λ_S, and derived 95% confidence intervals of λ_S using the standard deviation of the replicates (i.e. +/- 1.96* SD) .

We also computed vital rate sensitivity and elasticity, which allowed us to evaluate prospectively the potential for individual vital rates to contribute to population growth rate. As in McNew et al. (2012) and Dahlgren et al. (2016), we computed lower-level sensitivities and elasticities of each demographic rate that contributed to the stage-specific survivals and fecundities. This allowed us to evaluate potential contributions of component vital rates such as clutch size and nest success to population growth, in addition to the individual matrix elements. Also following McNew et al. (2012), we summed elasticities for vital rates that contributed to higher-level demographic processes (e.g. brood success and chick survival), and across age classes, to evaluate their net potential to affect population growth.

Finally, we conducted focused parameter perturbations of our population model to evaluate the potential for forest stand characteristics to influence spruce grouse population growth. For each stand variable (treatment type or age class) that was supported in a demographic analysis, we predicted a vital rate estimate from the covariate relationship associated with either high use (75% for a positive effect) or low use (25% for a negative effect) of the stand type. We substituted this value into our projection matrix as appropriate, and recalculated λ_D for the modified matrix. We then compared the change in λ_D relative to the mean vital rate matrix as an assessment of the potential for each supported stand characteristic to influence spruce grouse population growth in the system. This approach gives an assessment of stand type importance that considers both the strength of the covariate relationship from the demographic analysis and the potential for the individual vital rates to contribute to population growth based on the population model.

RESULTS

We captured 203 unique spruce grouse from 2012 through 2017, including 110 females and 93 males. Fifty two were juveniles captured during late summer and fall, 2014-2017, and 151 were adults. We radio-marked 150 of these spruce grouse. A full breakdown of age and sex classes, by year, along with samples of radio-marked birds, is provided in Table 2.

Table 2. Summary of spruce grouse captured, by age and sex class, during each study year in the Telos Region of northern Maine. The number of individuals that were radio-marked are indicated in parentheses.

Sex	Age Class[a]	2012	2013	2014	2015	2016	2017
Female	Adult	16 (16)	14 (12)	16 (13)	11 (11)	12 (11)	7 (7)
Female	Juvenile	0 (0)	0 (0)	5 (4)	15 (14)	9 (8)	5 (4)
Male	Adult	17 (1)	17 (0)	12 (4)	7 (7)	14 (14)	8 (7)
Male	Juvenile	0 (0)	0 (0)	4 (3)	4 (4)	6 (6)	4 (4)

[a] Juvenile = prior to first breeding season, Adult = entered first or later breeding season. Birds marked as juveniles 'graduated' into the adult age class in April of their first breeding season and thereafter contributed data as adults.

Nest Success

We located and conducted formal monitoring of 26 spruce grouse nests during phase 2 of the project, including 8 nests in 2015, 7 in 2016, 7 in 2017, and 4 in 2018. Nine of these nests failed, while 17 nests were successful. Based on egg floatation, the mean nest initiation date was 16 May. The earliest nest was initiated (first egg laid) on May 7th in 2016, while the latest nest was initiated on June 5th during the same year. Estimated and observed hatching dates ranged from June 10th to July 5th. Mean clutch size was 5.87 and ranged from 4 to 7 eggs.

We found little support for effects of nest initiation date or year on the daily nest survival rate (Table 3), and so used an intercept-only model as our base model structure. Mean daily nest survival was 0.980 (0.007 SE) which results in a 32-day estimate of nest success of 0.524 (+/- 0.11 SE). We found 8 nests in untreated clearcuts, 7 nests in treated clearcuts, 6 nests in residual stands, and 5 nests outside of these three stand treatment types. Ten nests were located in stands that were 20 or fewer years post-harvest, 4 nests occurred in stands 21-30 years post-harvest, and 12

nests were in stands 31 years post-harvest or older. We lacked stand age data for 1

nest.

The only stand characteristic associated with daily nest survival was treated

clearcuts (Table 3), which had lower daily survival probability compared with all other

stand types (β = -1.558 +/- 0.683). Nests located in clearcuts that received post-harvest

herbicide and/or thinning had a daily nest survival probability of 0.948 +/- 0.023 SE,

while nests located outside of these stands had a daily survival probability of 0.989 +/-

0.006 (Fig. 2). Those differences in daily survival probability predict that 18.4% of nests

in treated clearcuts were likely to be successful, compared with 69.5% of nests in other

stand types.

Table 3. Model selection results for analysis of spruce grouse daily nest survival in the Telos area of northern Maine, using data collected from 2015-2017.

Model[a]	AICc	ΔAICc	w_i	Dev.	k
Treated clearcut	58.66	0.00	0.51	54.63	2
Null	61.68	3.02	0.11	59.67	1
31+ year stand age	61.90	3.23	0.10	57.87	2
21-30 year stand age	63.05	4.39	0.06	59.02	2
Clearcut (untreated)	63.06	4.40	0.06	59.03	2
Residual stands	63.18	4.52	0.05	59.16	2
0-20 year stand age	63.19	4.53	0.05	59.16	2
Nest initiation date	63.69	5.03	0.04	59.66	2
Year	65.91	7.25	0.01	57.82	4

[a] Models generally contained covariates that described variation in characteristics of forest stands within which nests were located. These included stand treatment type (described in Table 2) and time since last harvest (stand age). We also evaluated effects of nest initiation date and year, and an intercept-only null model.
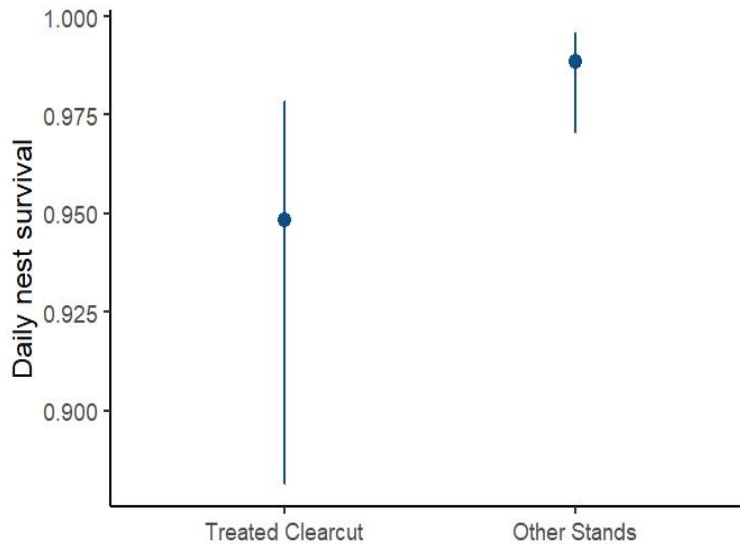
Figure 2. Comparison of daily nest survival probabilities for spruce grouse nests located in regenerating clearcuts that received post-harvest treatment in the form of herbicide and pre-commercial thinning (Treated Clearcut) and all other stands. Daily nest survival probability was estimated from 26 spruce grouse nests found in the Telos Region of northern Maine. Error bars represent 95% confidence intervals of daily nest survival estimates.

Brood Success

We monitored 60 spruce grouse broods over the duration of the study, including 15 in 2012, 7 in 2013, 7 in 2014, 11 in 2015, 13 in 2016, and 7 in 2017. Mean brood size during the last two weeks of August was 2.76 chicks/female. We collected 895 locations of females associated with broods (mean = 14.9 locations/female; range = 4 to 41 locations), including 671 locations of confirmed broods that were used for stand classifications. Brood locations were dispersed across all three treatment types and age classes, and sampling within stand categories was even across study years. Mean weekly detection probability differed between phase 1 of the study (p = 0.739+/- 0.033) and phase 2 (p = 0.623 +/- 0.039). We found model selection support for a year effect on brood success (Table 4), which showed that the weekly probability of brood survival

was lowest during 2014 (Φ_{week} = 0.871 +/- 0.059 SE) and greatest during 2012 (Φ_{week} = 0.987 +/- 0.012 SE; Fig. 3). This translated to an estimated mean brood success (proportion of broods that remained active with ≥1 chick at the end of August) of 0.548 (+/- 0.009 SE), and annual values ranged from 0.251 to 0.877. We found support for a positive effect of residual stand use on weekly brood survival (β= 0.819 +/- 0.415 SE; Fig. 4) while all other treatment type and stand age class covariates were not supported (Table 4).

Table 4. Model selection results for analysis of spruce grouse weekly brood survival probability in the Telos area of northern Maine, using data collected from 2012-2017. Brood survival was modeled using a CJS live encounter analysis, where apparent survival (Φ) represented the probability that a brood remained active (≥1 chick) during each 1-week interval, and detection probability (p) was the joint probability of failure to observe the radio-marked female and failure to observe chicks, given the brood remained active.

Model[a]	AICc	ΔAICc	w_i	Deviance	K
Φ (Residual + Year) p (Phase)	626.92	0.00	0.46	608.34	9
Φ (Year) p (Phase)	629.39	2.47	0.13	495.42	8
Φ (Stand Age 3 + Year) p (Phase)	630.61	3.69	0.07	612.03	9
Φ (Treated CC + Year) p (Phase)	630.71	3.79	0.07	612.13	9
Φ (Stand Age 1 + Year) p (Phase)	630.88	3.95	0.06	612.30	9
Φ (Null) p (Phase)	631.11	4.19	0.06	507.52	3
Φ (Stand Age 2 + Year) p (Phase)	631.41	4.48	0.05	612.83	9
Φ (Clearcut + Year) p (Phase)	631.49	4.57	0.05	612.92	9
Φ (Year) p (Null)	632.40	5.48	0.03	500.53	7
Φ (Year) p (Year)	633.41	6.49	0.02	490.89	12

[a] *Stand treatment types (Residual, Treated Clearcut (CC), and Clearcut) are described in Table 1. Stand age classes (Age 1, 2, and 3) correspond with 0-20, 21-30, and 31+ years post-harvest, respectively. Phase = study phase, 2012-2014 vs 2015-2017.*
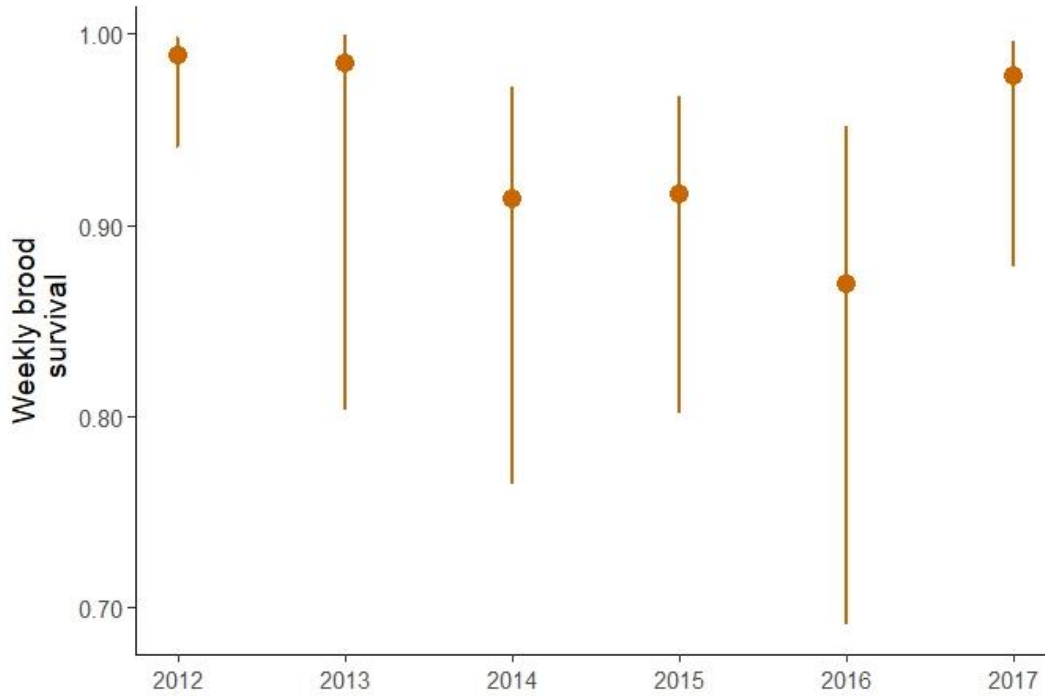
Figure 3. Annual estimates of weekly brood survival probability for radio-tracked spruce grouse broods in the Telos region of Northern Maine. Estimates were derived from a CJS capture-mark-recapture analysis that accounted for imperfect detection of chicks during brood checks. Brood survival probability reflected the weekly probability that a female with a brood retained ≥1 chick. Error bars represent standard errors.
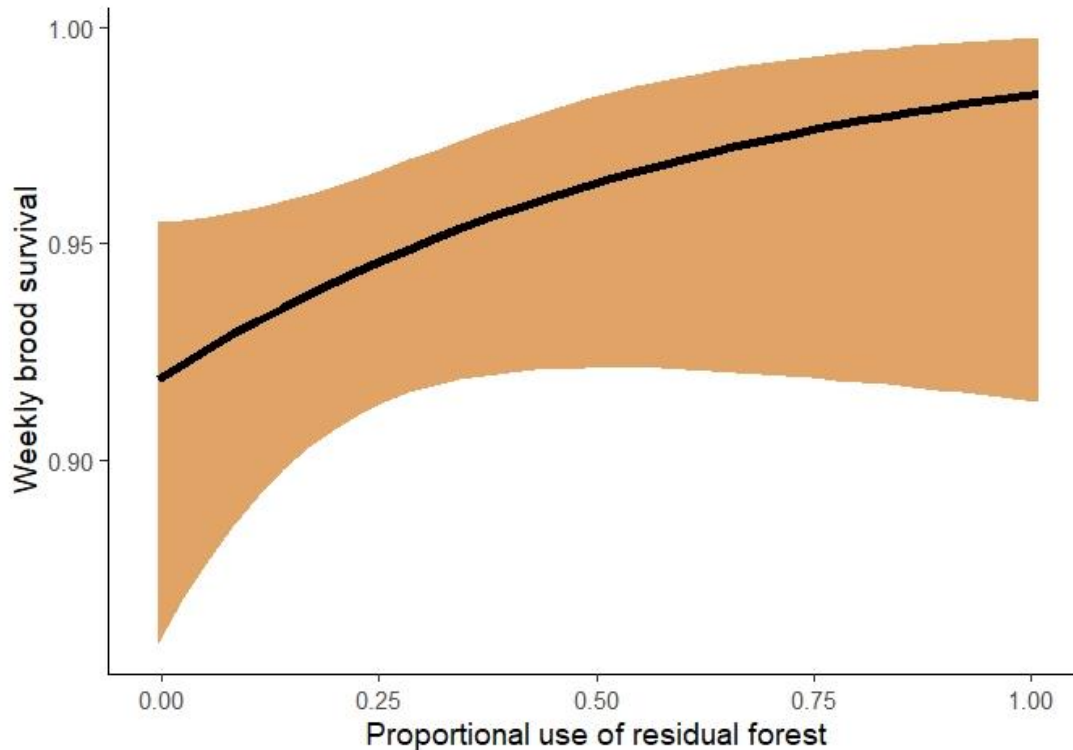
Figure 4. Predicted effect of proportional use of residual forest stands on the probability of brood survival probability for radio-tracked spruce grouse broods in the Telos region of Northern Maine. Estimates were derived from a CJS capture-mark-recapture analysis that accounted for imperfect detection of chicks during brood checks. Brood survival probability reflected the weekly probability that a female with a brood retained ≥1 chick. The gray ribbon reflects 95% confidence intervals.

Juvenile Survival

We monitored survival of 43 juvenile spruce grouse, including 27 females and 16 males. Twenty-two birds survived from independence to first breeding, whereas we detected mortalities for the remaining 21. We collected 244 locations from these birds (mean = 5.67 locations/bird). We found generally greater use of residual forest stands by juvenile spruce grouse compared to treated and un-treated clearcuts; however, we observed relatively high proportional use by some individuals within all three stand treatment types and age classes. We did notice particularly high use of residual forest

stands by juvenile spruce grouse during one study year (2015); however, including year and proportional use of residual stands as additive effects in a common model did not affect the estimates from either, suggesting no confounding influence of year on residual stand effects.

Model selection suggested an effect of sex on juvenile survival (Table 5), which suggested that males had greater survival than females (β=0.752 +/- 0.533 SE). Although the 85% confidence intervals of this effect overlapped 0.0, we retained the effect in subsequent models to account for any confounding variation associated with sex, given that we had relatively modest sample sizes for each group. An effect of year was not supported (Table 5), however annual estimates of juvenile monthly survival from the year model ranged from a low in 2015 of 0.857 +/- 0.042 to a high of 0.945 +/- 0.031 in 2017 (Fig. 5). Mean monthly juvenile survival across all four years of data was 0.892 +/- 0.022 SE, and cumulative survival across the 8-month juvenile survival interval was 0.400 +/- 0.080. We found that juvenile survival was negatively associated with proportional use of residual forest stands (β=-0.638 +/- 0.251; Fig. 6), while no other variables ranked within 2.0 ΔAIC_c of the best-supported model (Table 5).

Table 5. Model selection results for analysis of monthly survival of juvenile spruce grouse for the period between independence (Sep 1) and first breeding (May) in the Telos area of northern Maine, using data collected from 2014-2017. Juvenile survival was modeled using nest survival analysis, and we explored effects of forest stand harvest history (treatment type and time since harvest) on monthly survival probabilities.

Model	AICc	ΔAICc	w_i	Dev.	k
Sex + Residual	115.81	0.00	0.59	109.69	3
Sex + Clearcut	119.09	3.29	0.11	112.98	3
Sex + Treated CC	119.62	3.81	0.09	113.50	3
Sex	120.37	4.56	0.06	116.31	2
Null	120.53	4.72	0.06	118.51	1
Sex + Stand Age 3	121.94	6.13	0.03	115.82	3
Sex + Stand Age 1	122.09	6.29	0.03	115.98	3
Sex + Stand Age 2	122.29	6.48	0.02	116.17	3
Year	123.48	7.67	0.01	115.28	4
Year + Sex	124.42	8.61	0.01	114.13	5
Month	129.55	13.74	0.00	108.45	9
Year + Month	133.27	17.47	0.00	105.44	12

[a] *Stand treatment types (Residual, Treated Clearcut (CC), and Clearcut) are described in Table 1. Stand age classes (Age 1, 2, and 3) correspond with 0-20, 21-30, and 31+ years post-harvest, respectively.*
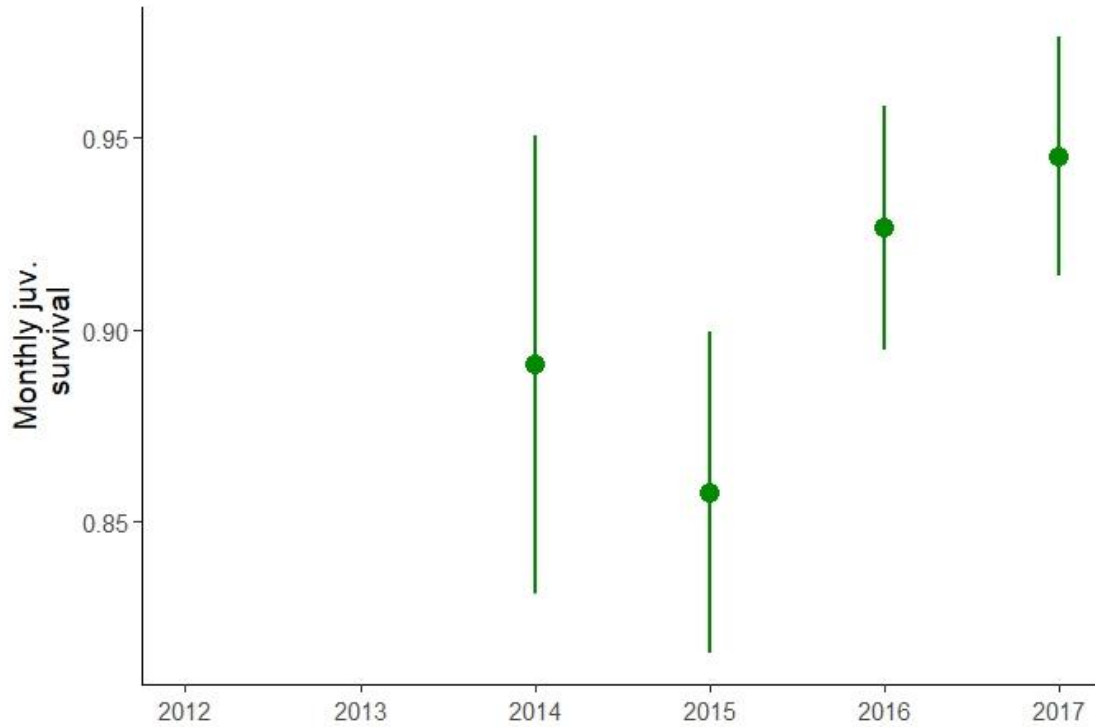
Figure 5. Estimates of monthly survival of juvenile (<1 year of age) spruce grouse radio-marked in the Telos region of northern Maine from 2014-2017. Estimates reflect the mean monthly probability of survival during September through May for each year that juveniles were monitored. Error bars represent standard errors (SE). Juvenile survival data were not available for 2012 and 2013.
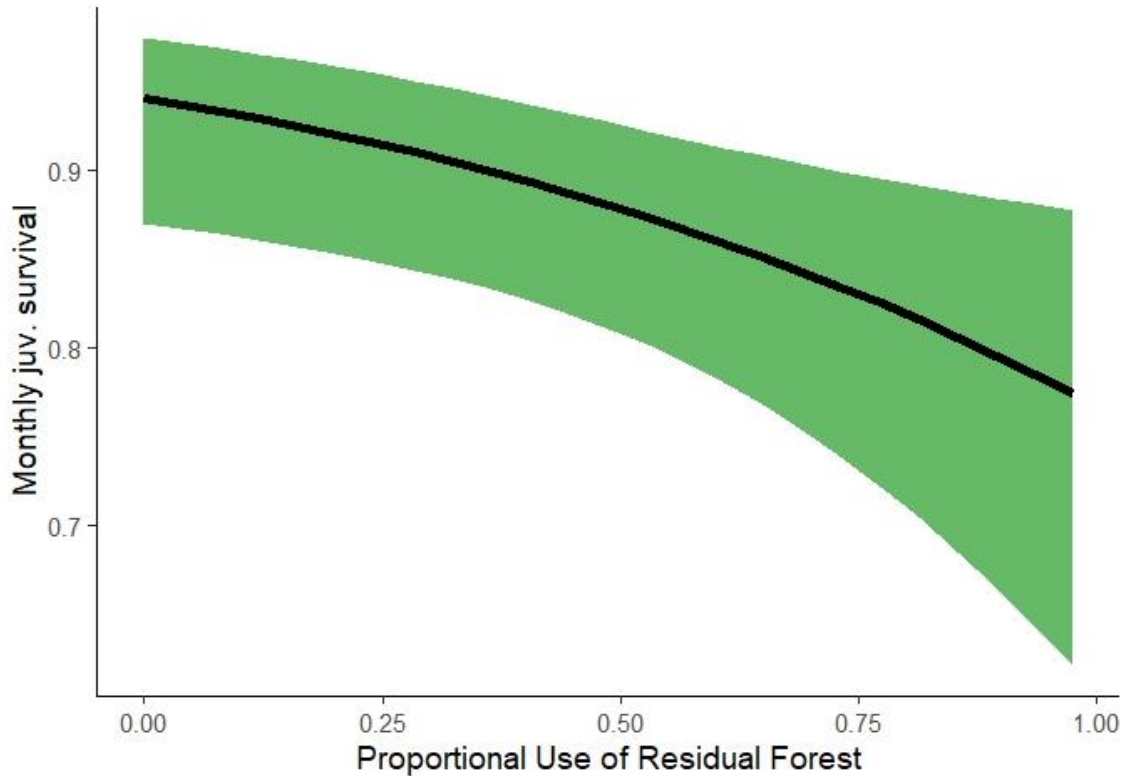
Figure 6. Predicted effect of proportional use of residual forest stands on monthly survival of juvenile (<1 year of age) spruce grouse radio-marked in the Telos region of northern Maine from 2014-2017. Estimates reflect the mean monthly probability of survival during September through May for each year that juveniles were monitored, and proportional use was estimated from the proportion of locations for each individual that occurred within stands without history of harvest since at least 1982. The gray ribbon reflects 95% confidence intervals of the estimates.

Adult Survival

We monitored survival of 116 adult spruce grouse, including 77 females and 39 males. We detected mortality for 49 birds, whereas 67 of them remained alive when their radio-transmitter failed or the study ended. We collected 1940 locations from these birds (mean = 16.7 locations/bird; range = 0 to 50 locations). Adult spruce grouse made greater proportional use of treated clearcuts than the other two stand types; however,

we observed a range of proportional use by individual birds across all stand types, with no indication of uneven sampling among years.

We found that a model containing a sex effect on adult survival was competitive with an intercept-only null model (Table 6), suggesting again that males had greater monthly survival compared with females (β=0.334 +/- 0.324 SE). As with the juvenile survival, 85% confidence intervals of this effect widely overlap 0.0, so while we retained it in subsequent models we do not interpret differences in survival among the sexes. We also found little model selection support for a year effect, but estimates from a year model suggested that mean monthly survival ranged from a high of 0.968 +/- 0.014 SE during 2017 to a low of 0.927 +/- 0.018 SE in 2016 (Fig. 7). This translated to a mean annual survival estimate 0.515 (+/- 0.050 SE), with annual estimates that ranged from 0.400 to 0.673. We found that adult survival was positively associated with proportional use of untreated clearcuts (β=0.421 +/- 0.191; Fig. 8), while no other variables ranked within 2.0 ΔAIC_c of the best-supported model (Table 6).

Table 6. Model selection results for analysis of monthly survival of adult spruce grouse monitored in the Telos area of northern Maine, using data collected from 2012-2017. Adult survival was modeled using nest survival analysis, and we explored effects of forest stand harvest history (treatment type and time since harvest) on monthly survival probabilities.

Model[a]	AICc	ΔAICc	w_i	Dev.	k
Sex + Clearcut	326.50	0.00	0.52	320.48	3
Null	329.15	2.65	0.14	327.15	1
Sex	330.05	3.55	0.09	326.04	2
Sex + Stand Age 1	330.18	3.68	0.08	324.15	3
Sex + Stand Age 3	331.16	4.66	0.05	325.13	3
Sex + Treated CC	331.63	5.13	0.04	325.60	3
Sex + Residual	331.90	5.39	0.04	325.87	3
Sex + Stand Age 2	332.07	5.56	0.03	326.04	3
Year	334.52	8.01	0.01	322.42	6
Month	339.35	12.84	0.00	314.98	12
Year + Month	345.12	18.62	0.00	310.39	17

[a] Stand treatment types (Residual, Treated Clearcut (CC), and Clearcut) are described in Table 1. Stand age classes (Age 1, 2, and 3) correspond with 0-20, 21-30, and 31+ years post-harvest, respectively.
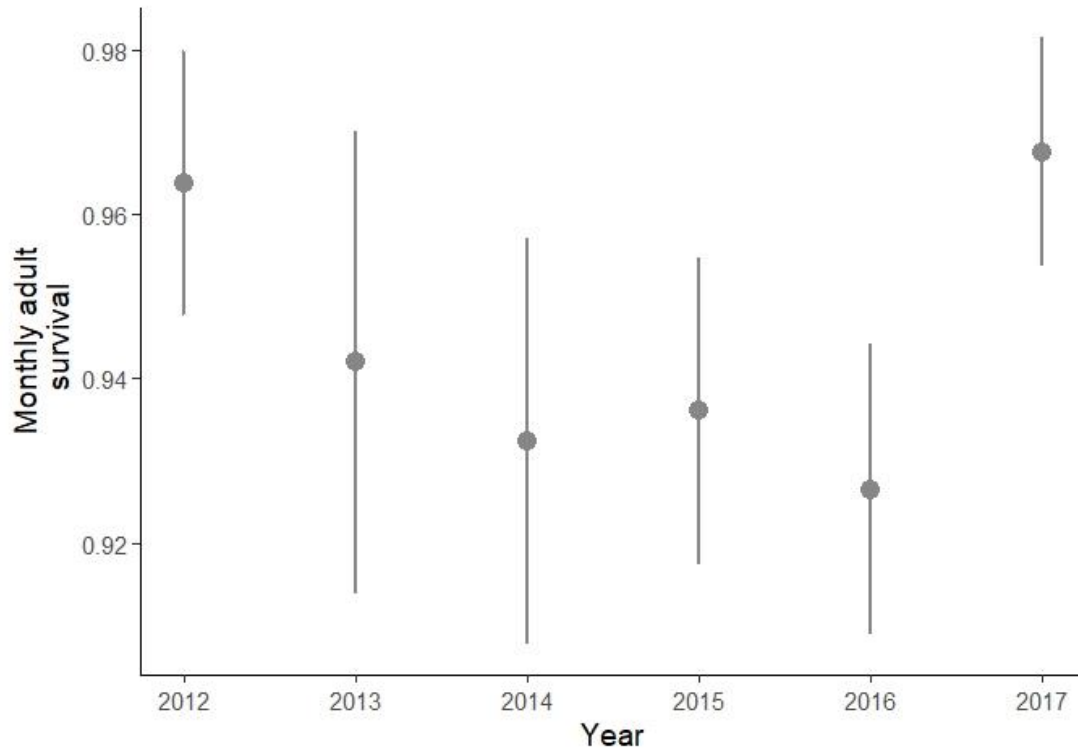
Figure 7. Estimates of monthly survival of adult (>1 year of age) spruce grouse radio-marked in the Telos region of northern Maine from 2012-2017. Estimates reflect the mean monthly probability of survival from May through April for each year. Error bars represent standard errors (SE).
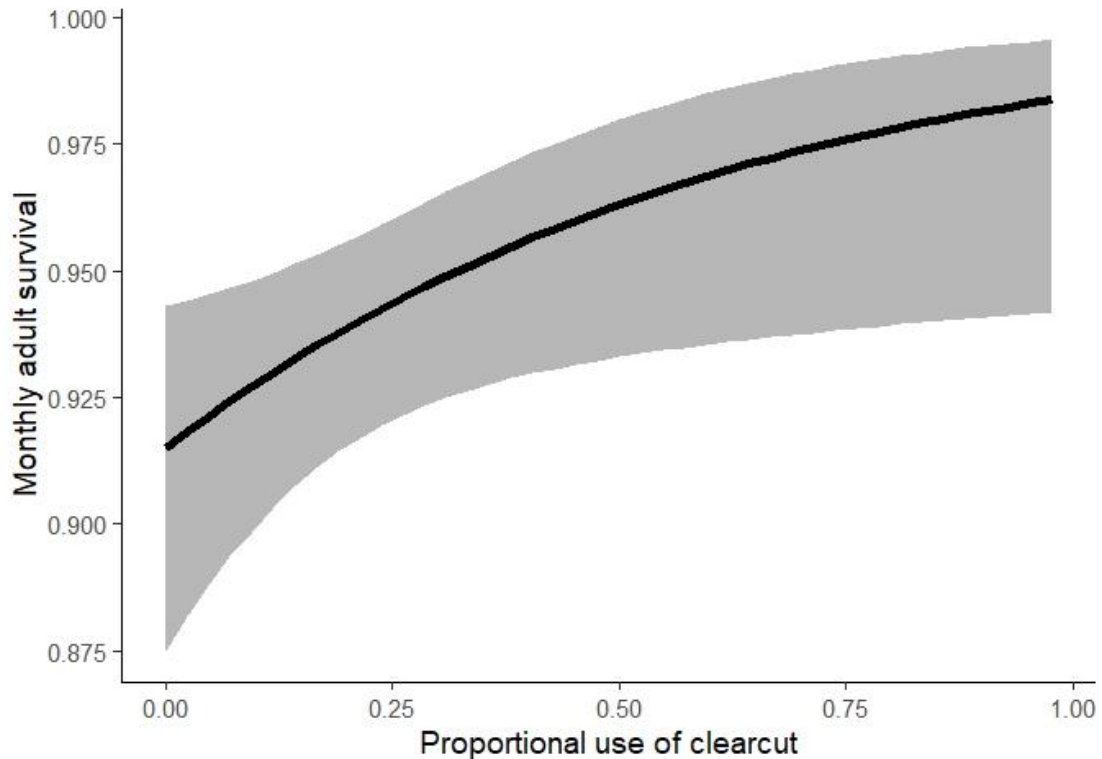
Figure 8. Predicted effect of proportional use of clearcut stands that did not receive post-harvest treatment on monthly survival of adult (>1 year of age) spruce grouse radio-marked in the Telos region of northern Maine from 2012-2017. Estimates reflect the mean monthly probability of survival during May through June each year, and proportional use was estimated from the proportion of locations for each individual that occurred within stands that were clearcut since 1982 and did not receive subsequent thinning or herbicide application. The gray ribbon reflects 95% confidence intervals of survival estimates.

Population Model

A deterministic projection model based on mean values for each of vital rate (Table 7) returned a predicted growth rate of $\lambda=0.714$, suggesting a substantial decline. The 95% confidence intervals from a stochastic model based on annual variation in vital rates (Table 8) predicted a slightly lower growth rate, and confirmed that the predicted trend was less than 1.0 ($\lambda = 0.680$; 95% CI = 0.588 to 0.771). Annual vital rate values

predicted population increase during only one of the six study years, although a second

year approached a value of 1.0 suggesting population stability that year (Table 8).

Based on both vital rate sensitivity and elasticity analysis from the deterministic

model, annual survival of adults had the single greatest potential to effect the population

growth rate, with juvenile survival and vital rates associated with brood-rearing (brood

success and chick survival) having more moderate sensitivities and elasticities for

individual vital rates (Table 7, Figure 9). The summed elasticity associated with all

aspects of nesting was 0.580, with generally equal importance of characteristics of the

nesting attempt (nesting and renesting rates, nest success; sum elasticity = 0.277) and

eggs (clutch size and hatchability; sum elasticity = 0.303). The summed elasticity

associated with the brood-rearing period (brood success, chick survival; sum elasticity =

0.303) was roughly equivalent to either nest- or egg-summed elasticity values. By

comparison, elasticity for adult annual survival was 0.56, and for juvenile survival was

0.15. Overall, adult survival and components of nesting had the greatest potential to

influence spruce grouse population growth, with more moderate importance of brood-

rearing and comparably low importance of juvenile survival (Figure 9C).

Single parameter perturbations of the population model showed that altering adult

survival to reflect 75% use of untreated clearcuts produced the largest increase (0.249)

in population growth (λ=0.963) relative to the baseline population mean (Table 9, Figure

9B). For all other single vital rate perturbations, increased use of favorable forest

stands increased population growth, but to lesser extents (Table 9, Figure 9B). When

all 5 perturbation scenarios were combined, the resulting model predicted positive

population growth (λ=1.120; Table 9).

Table 7. Summary of mean vital rate estimates and SE used to construct a deterministic stage-structured population model for spruce grouse in the Telos region of northern Maine, along with results of vital rate sensitivity and elasticity analysis for each vital rate.

Vital Rate	Age Class	Value	SE	Sensitivity	Elasticity
Nesting Propensity	Juvenile	1.00	-	0.06	0.05
Nest Success	Juvenile	0.52	0.11	0.08	0.03
Clutch Size (1st)	Juvenile	5.87	0.97	0.01	0.04
Egg Hatchability	Juvenile	0.90	0.00	0.07	0.05
Brood Success	Juvenile	0.55	0.05	0.12	0.05
Chick Survival	Juvenile	0.52	-	0.12	0.05
Renesting Prob.	Juvenile	0.25	-	0.04	0.01
Clutch Size (2nd)	Juvenile	4.87	0.97	0.00	0.01
Nesting Propensity	Adult	1.00	-	0.15	0.11
Nest Success	Adult	0.52	0.11	0.19	0.07
Clutch Size (1st)	Adult	5.87	0.97	0.02	0.09
Egg Hatchability	Adult	0.90	-	0.17	0.11
Brood Success	Adult	0.55	0.05	0.27	0.11
Chick Survival	Adult	0.52	-	0.29	0.11
Renesting Prob.	Adult	0.25	-	0.09	0.02
Clutch Size (2nd)	Adult	4.87	0.97	0.00	0.02
Survival (8 month)[a]	Juvenile	0.45	0.08	0.33	0.15
Survival (annual)[a]	Adult	0.50	0.05	0.70	0.56

[a] for elasticity estimates of Juvenile and adult survival, we used the sum of the lower-level elasticities of these terms for both the upper and lower matrix elements (McNew et al. 2012, Mills 2013, Dahlgren et al. 2016).

Table 8. Year-specific vital rate estimates used to construct a stochastic stage-structured population model for spruce grouse in the Telos region of northern Maine, along with estimates of annual population growth (λ) associated with vital rates for each study year.

Year	Brood Success	Juv. Survival[a]	Adult Survival	F_{Juv}	F_{Ad}	λ
2012	0.894	0.450	0.642	0.346	0.552	0.980
2013	0.854	0.450	0.488	0.331	0.430	0.808
2014	0.406	0.396	0.393	0.139	0.174	0.524
2015	0.415	0.293	0.388	0.105	0.176	0.486
2016	0.246	0.543	0.308	0.115	0.088	0.416
2017	0.797	0.636	0.608	0.437	0.473	1.034

[a] *Estimates of Juvenile survival for years 1 and 2 included at mean value because we lacked estimates for those years.*

Table 9. Vital rates and resulting population growth rate (λ) from single parameter perturbations of a stage-structured population model for spruce grouse in the Telos region of northern Maine. Scenarios for parameter perturbations changed each vital rate to reflect increased positive use of forest stand types that were associated with stage-specific vital rates based on demographic analyses.

| Scenario	F_{Juv}	F_{Ad}	S_{Juv}	S_{Ad}	λ
Baseline – mean value for all vital rates.	0.212	0.298	0.357	0.502	0.714
Nests not located in treated clearcuts	0.258	0.363	0.357	0.502	0.760
Broods with 75% residual stand use	0.304	0.427	0.357	0.502	0.806
Juvenile birds with 25% residual stand use	0.231	0.298	0.389	0.502	0.733
Adult birds with 75% untreated clearcut use	0.212	0.390	0.409	0.751	0.963
All parameter perturbations applied	0.403	0.680	0.389	0.751	1.120
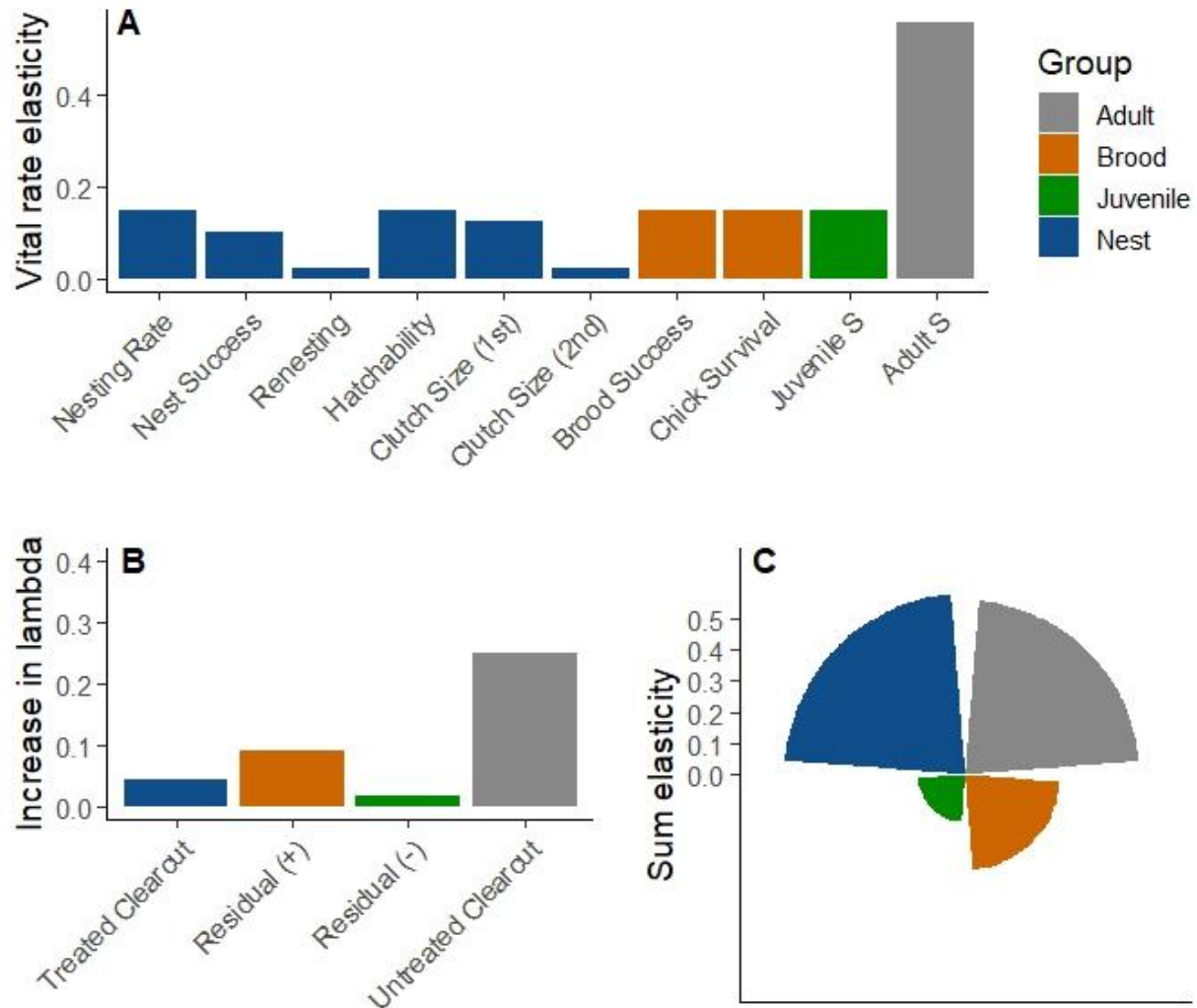
Figure 9. Results of elasticity analysis evaluating the relative importance of spruce grouse vital rates to population growth. Panel A) gives the elasticity value (relative potential contribution to lambda) for individual vital rates, where color groupings indicate individual vital rates associated with a particular life stage (nesting, brood-rearing, juvenile, and adult). Panel B) gives the results of single parameter perturbations to evaluate combined effects of forest stand characteristics and vital rate elasticities on population growth, where color coding again demonstrates each particular life phase. Panel C) demonstrates relative differences in the summed elasticities for all vital rates associated with each life phase, based on the size of each slice of the pie.

DISCUSSION

Spruce Grouse Population Status in Maine

We found that spruce grouse demographic rates, as estimated during our study, were consistent with an overall decline in the population. Prior to our study relatively little information existed to assess spruce grouse population status in Maine. Working in our study system, Dunham (2016) found that occupancy of conifer stands by territorial male spruce grouse was relatively stable over a 3-year survey period (phase 1 of our study), however over short time periods occupancy (proportion of sites with ≥1 individual) should be relatively stable and may not reliably reflect changes in abundance within sites. Over nearly 40-years in the Adirondack mountains of New York, Ross et al. (2016) documented substantial declines in spruce grouse occupancy of lowland conifer stands. Similarly, Gilbert and Blomberg (2019) found a nearly 50% reduction in stand occupancy by spruce grouse on Mount Desert Island, Maine, between the early 1990s and 2017. In the Mount Desert Island study system, the apparent abundance of spruce grouse also declined substantially during that time period (Gilbert and Blomberg 2019). Outside of the Northeastern U.S., Anich et al. (2013) found that demographic rates of spruce grouse in northern Wisconsin predicted an annual growth rate of $\lambda=0.68$; this finding closely matches results from our system using a similar approach.

Evidence from our elasticity analyses suggests that adult female survival is the demographic rate with the greatest potential to influence spruce grouse population growth. This is not to necessarily say that low adult survival was responsible for the declining values of λ we estimated (Cooch et al 2001), but it is certainly one possibility, and adult survival is also the vital rate with the greatest potential to affect positive future

population growth. Our estimate of spruce grouse annual survival (~50%) was nearly double that recently reported for ruffed grouse (*Bonasa umbellus*) in Maine (~28%; Davis et al. 2018), but greater annual survival for spruce grouse is expected given their relatively slower life history strategy (Schroeder et al. 2018). A variety of survival estimates exist in the literature for adult spruce grouse, and range from a low of 39% for spruce grouse on Prince of Wales Island in Alaska (Nelson 2010) to a high of 63% in southwestern Alberta (Keppie 1979). Varied methods for survival estimation (e.g. band returns, age-ratios, radio-telemetry) may complicate interpretation of differences in survival estimates among studies. Recently, Anich et al. (2013) used radio-telemetry to estimate survival of adult female spruce grouse in northern Wisconsin, and reported a slightly lower estimate (40%) of survival than we found for Maine.

Components of reproduction also had relatively large potential to affect population growth when considered as aggregate components of the reproductive process (nesting, brood rearing). Estimates of nest success from the literature are highly variable and range from 29-81% (Schroeder et al. 2018), however many of these values are based on apparent nest success, which is inherently biased high (Mayfield 1975). Anich et al. (2013) calculated a daily nest survival rate for spruce grouse in Wisconsin of 0.985, for a 32-day nest success estimate of 61.6%; slightly greater but comparable to our estimate of 52.4%. Estimates of brood success or chick survival are less commonly reported in the literature than measures of annual productivity (e.g. chicks/female). During our study, the mean number of chicks in each brood at the end of August was 2.76. When multiplied by our estimated brood success rate, this translates to an estimate of chicks per hatched nest of 1.52, and when discounted to reflect overall nest

success, returns an estimate of 0.97 chicks per female in the population. This is among the low end for estimates from the literature, which range from 1.1 to 4.4 (Schroder et al. 2018). Working in New Brunswick, Keppie (1982) estimated mean brood size of 3.3 chicks/brood, which gives the closest regional comparison, albeit more than 35 years previous to our work. Therefore, production of chicks during our study had a moderate potential to influence λ, and was also below average relative to values reported for the species elsewhere. Collectively our results, in comparison with the literature, suggest that adult survival and/or survival of chicks into the juvenile cohort contributed to the conclusion of a declining population during our study.

Forest Management and Spruce Grouse Demographics

We found that a variety of silvicultural practices in conifer stands were associated with spruce grouse demographic rates. However, the specific relationships varied considerably depending on stand treatment type and life phase, with each of the three treatment types having effects at one or more life phase. Clearcuts that received post-harvest treatments of either herbicide or pre-commercial thinning were negatively associated with nest success. Among our stand-level results, this should be interpreted most cautiously because of the modest number of nests found during our study. Nevertheless, we did observe that nests located in treated clearcuts (n=7) failed more frequently than nests in other stand types. Nest success of ground-nesting galliforms in eastern North America has been previously documented to be enhanced by visual obscurity provided by dense vegetation near the nest (Lehman et al. 2008, Fuller et al. 2013). Based on field observations, clearcut stands with post-harvest treatments of herbicide and PCT typically lacked substantial ground cover and nests were more

exposed compared with other sites. In fact, previous comparisons of untreated

clearcuts versus clearcuts with post-harvest treatments of herbicide and PCT on our

study area indicated less visual obstruction at ground level and fewer understory woody

stems in stands with post-harvest treatments (Homyack et al. 2004). Thus, inadequate

cover to obscure nests within clearcuts treated with herbicide and PCT may explain

lower nest success there, given that nest failure during our study was almost exclusively

associated with nest depredation. It is also important to recognize, however, that during

phase 1 of the project, Dunham (2016) found that treated clearcuts harbored the highest

density of and greatest occupancy by territorial males, so this stand type may provide

additional population benefits to life stages outside of nesting that we did not address in

this report. Alternatively, clearcuts with post-harvest treatments could also have

features that attract birds for courtship, display, and nesting, but which may compromise

subsequent nest success because of inadequate nest concealment.

Females that made greater use of residual stands for brood rearing experienced

higher brood success, however, juvenile birds had lower survival in this same stand

type after achieving independence from their mothers. We did not regularly follow the

same individual birds between brood rearing and post-independence, so these results

do not represent a direct relationship between brood-rearing habitat and areas used by

juveniles. Rather it suggests that at the landscape level, residual forest stands without

a recent harvest history likely provide a net positive benefit to broods, but may have an

offsetting negative effect on survival of young spruce grouse after they reach

independence. Previous work on our study site (Fuller et al. 2004) documented greater

canopy closure and tree basal area in mixed conifer-deciduous and conifer stands

without a recent history of forest harvest compared to regenerating clearcuts, which suggests that residual stands may provide potential protection to mothers and broods from raptors, which are thought to be a frequent cause of spruce grouse mortality. Why juveniles experienced lower survival in residual stands after brood break-up is uncertain, however, lower lateral foliage density in residual mixed (42%) and conifer (32%) stands relative to clearcut (70%) stands (Fuller et al. 2004) suggests that understory cover may be insufficient to obscure juveniles from predators after they obtain larger size and are foraging independently. Thus, microsite-level conditions, and their interaction with resource requirements that are life-stage specific, may be responsible for the opposing relationships observed in residual stands between the brooding and juvenile phases.

Adult spruce grouse that made greater use of clearcuts which did not receive post-harvest treatments had higher survival compared to those with greater use of other stand types. Again, those results may be explained by greater cover and visual obscurity that could provide protection from predators in regenerating clearcuts. Fuller et al. (2004) documented higher lateral foliage density in regenerated clearcuts relative to mature mixed and conifer stands, and Homyack et al. (2004) reported greater lateral obscurity (i.e., shorter distance that cover boards would be completely obscured by vegetation from sampling points) in untreated clearcuts relative to clearcuts with post-harvest treatments of herbicide and PCT in our study region. Thus, the lower understory cover in clearcuts with common postharvest treatments (i.e., herbiciding followed by PCT) likely explains why spruce grouse survival was higher in untreated clearcuts.

Untreated clearcuts had greatest positive influence on potential growth rate of spruce grouse; however, there are two caveats to this result. First, our location data was primarily restricted to our late spring, summer, and early fall, and our inference about the effects of untreated clearcuts on survival of adult spruce grouse should be confined to that period. To that end, we collected relatively few locations during late fall, winter, and early spring, and seasonal differences in spruce grouse habitat relationships or behaviors could alter the effects of stand treatment types on adult survival across the full annual cycle. Second, because our analysis is based exclusively on spruce grouse use, our results are conditioned on spruce grouse selection of a particular area, which presumably occurs because it meets basic habitat requirements (e.g. conifer dominance within stands). As such, untreated clearcuts in the context of our data were restricted to those areas of the landscape that regenerated into conifer-dominated stands in the absence of post-harvest treatments to suppress deciduous growth (e.g. herbicide and PCT). Hence, our finding here does not support a positive effect of all clearcutting on spruce grouse survival, but rather those clearcuts (e.g., on areas of marginal site quality) that regenerate into conifer-dominated stands without additional management intervention. These caveats notwithstanding, we found that increased use of this stand type had the single greatest influence on spruce grouse population growth rate, which highlights the importance of this stand type within our study landscape. Historically, spruce budworm was the dominant disturbance in forest stands of northern Maine, and budworm-defoliated stands are typically characterized by high densities of understory conifer stems (Payer and Harrison 2000). Given that: 1) fires, hurricanes and other stand replacing disturbances are uncommon in this mesic portion of the geographic

range of spruce grouse (Lorimer 1977, Fraver et al. 2009); and 2) salvage harvesting and spraying have historically been used to reduce effects of spruce-budworm outbreaks (Legaard et al. 2015); clearcutting on sites conducive to conifer regeneration may be a useful management technique to enhance habitat use and survival by adult spruce grouse in commercially-managed landscapes.

Broad-scale trends away from clearcut harvesting and increased application of partial harvesting approaches may have negative consequences for spruce grouse conservation. Annual acreage of clearcutting in Maine has decreased since the enactment of the Maine Forest Practices Act in 1991. In contrast, the annual acreages of partial harvesting have increased drastically, and average annual forest harvesting footprint has more than doubled. The annual area of partial harvests alone have increased from 40,755 ha in 1988 to 221,753 ha in 2001, a more than five-fold increase (Maine Forest Service 2000-2015, Appendix A). Between 1982 and 2015 approximately 32% of Maine (2,934,732 of 9,164,673 ha) was harvested with a cumulative area of approximately 5,868,785 ha, and partial harvest accounted for 86% of that area. Approximately half of the harvested area reported as partially logged is recorded as some form of selection harvest, and Fuller et al. (2004) documented that managers preferentially removed large conifer trees when conducting selection harvests and that residual stand composition tended to shift towards deciduous trees. Robinson (2006, p. 30) reported fewer regenerating conifer saplings in stands after partial harvesting (i.e., included both selection and shelterwood harvests) compared to stands regenerated after clearcutting. Further, other studies from northern Maine and the region have reported lower conifer basal area (Fuller and Harrison 2007), lower

proportion of coniferous trees (Rolek et al. 2018), and lower coniferous sapling density

(Fuller and Harrison 2007) in partially harvested stands compared to residual stands.

Forest composition in northern Maine has shifted from conifer to deciduous-dominated

trees during the 3 decades preceding our study (1975- 2004; Legaard et al. 2015),

presumably in response to these practices. Further, extent of conifer-dominated stands

in the region has continued to decline (Simons-Legaard et al. 2016) and fragmentation

of residual conifer stands had increased (Simons-Legaard et al. 2018).

Spruce grouse do not typically occupy partially-harvested stands that lack conifer

dominance. Despite that partial harvests were common across our study area, we were

not able to evaluate their effect on survival because we did not observe substantial

spruce grouse use of those stands during any life history phase. We located only 4 of

26 nests (15%) in this stand type, and recorded only 9.2% of brood locations, 9.6% of

juvenile locations, and 6.4% of adult locations in partially harvested stands. Similarly,

Dunham (2016) found that territorial males did not occupy this stand type. Thus,

potential additive effects of the shift away from clearcutting, the continued trend towards

partial harvesting, decreasing size and increasing fragmentation of conifer stands,

coupled with trends towards increasing deciduous composition in forests of northern

Maine may present significant challenges for future conservation of spruce grouse in

this region.

In contrast to stand treatment type, we found little to no evidence that time since

harvest (stand age) was associated with any spruce grouse demographics. This is

perhaps not surprising, since the structure and composition of trees and other

vegetation within stands, and not age per se, is probably the greatest driver of spruce

grouse habitat associations. Because forest regeneration can be highly variable depending on site characteristics (e.g. soils, drainage), age may not be as reliable predictor of stand structure and composition. Alternatively, the stand age classes that we used may be too fine to reflect large changes in stand structure that were better captured by stand treatment types. Similarly, Rolek et al. (2018) reported that abundance and species richness of spruce-fir-associated songbirds in our region were strongly associated with harvest and post-harvest treatments, but were not reliably predicted by time since harvest. Given that other confounding variables such as site quality, drainage, and species composition prior to harvest all affect the rate, density, and composition of post-harvest regeneration, it is not surprising that spruce grouse demographics are more closely associated with harvest treatments than time since harvest.

Overall our results highlight the importance of considering habitat use throughout the full life cycle, because positive or negative effects associated with a particular forest characteristic at one life stage may not be consistent at all life stages. Furthermore, our population modelling highlights the importance of landscape heterogeneity in promoting spruce grouse population performance. In our system, no single stand type was associated with net positive population growth for spruce grouse, however, when each of the positive associations we observed for individual demographic rates were combined into a single population model, that model predicted population increase. Spruce grouse are conifer-obligate species, and so a critical mass of conifer-dominated stands within forest landscapes is the first pre-requisite to maintain spruce grouse populations.

Study Limitations

   Our study represents one of the most comprehensive demographic datasets on spruce grouse from anywhere within their range, and the best available data to give a current assessment of population status in Maine. Nevertheless, it is important that we acknowledge some limitations to be considered when interpreting our results.

   One caveat to our finding of support for a population decline is that even with 6 years of data we may not have captured the full range of annual variation in this system. If, by chance, our study period coincided with more years of poor population performance than is reflective of the longer-term average, we may have under-predicted the mean population growth rate. Throughout the core of their range spruce grouse populations exhibit cyclic dynamics that coincide with the boreal forest 10-year cycle (Martin et al. 2001). The extent to which these dynamics extend into the northeast and Maine specifically is unknown; however, spruce grouse cycles in the boreal region are typically correlated with cycles of snowshoe hares (Martin et al. 2001), which do not appear to exhibit strong cyclicity in the southeastern portion of their range (Murray et al. 2008), including Maine (Scott 2009). Our estimated annual growth rates for each study year seemed to follow a non-linear pattern, with higher growth rates during the first and last years of the study and lower projected growth rates during the central years (Table 8), suggesting that broader-scale temporal effects on population persistence may warrant additional considerations.

   We were also inherently limited in our ability to characterize fully the ecology of the species due to logistic constraints both unique to our system and that are relatively ubiquitous to wildlife ecology in general. For some vital rates, such as nest success and

clutch size, sample size limitations prevented us from deriving year-specific estimates, and this may have dampened the role of stochastic processes and caused us to under-estimate annual variation in population growth. In the case of juvenile survival, we were only able to estimate 4 years' worth of values, and we may have under- or over-estimated the true 6-year mean. We also had to rely on estimates and evidence from the literature to support some demographic rate values, such as rates of nesting and egg hatchability. Our sensitivity analysis suggested that many of these uncertain vital rates had a relatively low influence on λ, so the consequence of this potential error was likely minimal. Finally, we were also unable to characterize more complex population processes, such as density dependence, vital rate covariance, and stochastic processes, each of which may have moderating or cascading effects on population growth. Because of all of these reasons, our conclusion remains that spruce grouse populations are likely declining in our area consistent with larger regional patterns, but we caution rigid interpretation of our specific estimates of population growth for the reasons outlined above.

Conclusions and Recommendations

Our results, combined with those from other studies, suggest that spruce grouse populations are declining in Maine (Gilbert and Blomberg 2019), throughout the northeast (Ross et al. 2016) and at the southern edge of the species' range more generally (Anich et al. 2013). Long-term monitoring is needed to evaluate fully the vulnerability of the species along southern range margins, but such monitoring of spruce grouse populations can be challenging because of their cryptic nature and often-inaccessible habitat. In 2004, a survey of wildlife agencies conducted by Sands and

Pope (2010) showed that no central or eastern states conducted formal monitoring of spruce grouse. Since then, some monitoring programs have been implemented by a handful of states. For example, Minnesota has developed a monitoring protocol using winter counts of spruce grouse fecal pellets, which can be used to track stand occupancy (Roy et al. 2018), and New York maintains regular monitoring affiliated with their state's spruce grouse recovery plan (Ross and Johnson 2012). A focused population monitoring program in Maine using fecal sampling, callback surveys, or other methods should be implemented.

Our results demonstrate the potential for human land use (forest management decisions) to affect spruce grouse demographics and, in turn, influence population dynamics. Our conclusion that populations occurring within conifer-dominated stands, where we documented substantial use by radio-equipped grouse and their broods, were declining is concerning. Another important consideration is that, despite the prevalence of partial harvesting on our study area since 1995, we did not observed substantial use of partially harvested stands by spruce grouse during any life history stage, and thus could not directly evaluate the effect of that common harvest treatment on demographics. Given that predominance of partial harvesting in northern Maine during the past 3 decades, the typical shift of stands towards greater deciduous composition after partial harvests, and the documented recent decline of conifer-dominated forest and increasing fragmentation of residual conifer patches across northern Maine, we caution that habitat quality and quantity for spruce grouse is likely declining in the state. The additive effects of negative growth rates in conifer-dominated habitats, coupled with loss and fragmentation of conifer forest across the larger landscape could result in

significant future challenges for spruce grouse conservation in northern Maine. Our research provides a strong baseline to inform functional relationships between spruce grouse populations and expected land use change, and we suggest that further work explore these areas to assess population viability in a spatially-explicit manner. This may be particularly important as changing forest practices (e.g. Legaard et al. 2015) or climate change (e.g. Bose et al. 2017) continue to induce shifts in the conifer-dominated forests of the state, which will have cascading effects for conifer-dependent species (e.g. Simons-Legaard et al. 2016) like spruce grouse.

At present Maine's contains the largest expanse of habitat and likely the greatest abundance of spruce grouse in the northeastern United States. However, spruce grouse are not distributed contiguously throughout the state. The extent to which population connectivity and gene flow exists, particularly along the extreme southern range margin (i.e. Downeast and Central Maine), is unknown, as is connectivity with Canadian populations and the potential for immigration/emigration to mitigate population declines. Exploring how Maine's spruce grouse fit into the larger regional dynamics of the species will be important to understand how future declines of spruce grouse in Maine could affect the greater regional dynamics of the species.

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ADDITIONAL FUNDING APPLIED FOR

1. Demography and population status of spruce grouse in northern Maine forests. Maine Outdoor Heritage Fund. Co-PI with Dan Harrison. $17,835. *Successful.*
2. Demography and population status of spruce grouse, and relationships with forest management. Maine Department of Inland Fisheries and Wildlife. $100,537. *Unsuccessful.*
3. Linking habitation associations with demographics to inform conservation of spruce grouse throughout the northern forest. US Department of Agriculture Northeastern States Research Cooperative. $63,633. *Unsuccessful.*

PROJECT PRODUCTS TO DATE

In addition to the completed products below and this report, we anticipate a number of additional products over the next few years in the form of published peer-reviewed manuscripts, a PhD Dissertation, and additional opportunities for press, outreach, and professional presentations. The CFRU will be acknowledged in all future products associated with data collected during this project.

Press Coverage:

1. The project was profiled on the weekly radio program "The Maine Birding Trail" with Bob Duchene. July 2016.

Web Presence:

1. Information about spruce grouse research at the University of Maine, including this project, can be found at erik.blomberg.weebly.com/research/spruce-grouse

Professional Presentations:

1. Tebbenkamp, J.T., E.J. Blomberg, D.J. Harrison, and R.L. Holberton Is Autumnal Display Associated with Territorial Defense Or Mate Prospecting? A Case Study with Spruce Grouse. The Wildlife Society Annual Conference, Raleigh, NC. October 2016. Poster.
2. Parkhill, N.S., J.M. Tebbenkamp, *S.W. Dunham, D. J. Harrison, E.J. Blomberg. Effect of Forest Structure on Nest Site Selection by Spruce Grouse across Two Spatial Scales. The Wildlife Society Annual Conference, Raleigh, NC. October 2016. Poster.
3. Tebbenkamp, J., E. J. Blomberg, D. Harrison, R. B. Allen, and K. Sullivan. Spruce grouse demography and population status in commercially harvested forests of Northern Maine. Poster. Maine Cooperative Fish and Wildlife Research Unit Annual Meeting. Orono, ME, March 2016.
4. Blomberg, E.J., J. Tebbenkamp, S Dunham, and D.J. Harrison. The role of forest disturbance in habitat relationships and population ecology of Spruce Grouse. Midwest Fire Science Consortium Webinar Series. January 2019.
5. Blomberg, E.J. Understanding population process to inform bird conservation in human-altered landscapes. Invited Seminar, University of Rhode Island. February 2019.
6. Blomberg, E.J., J. Tebbenkamp, S Dunham, and D.J. Harrison. 2019. Spruce grouse demographics in the commercially managed forests of northern Maine. Final project report presented to Advisory Committee of Maine Cooperative Forestry Research Unit, Orono, Maine. 11 April.

7. Blomberg, E.J., J. Tebbenkamp, S Dunham, and D.J. Harrison. Population Ecology of Spruce Grouse in Commercially-managed Forests. American Ornithological Society Annual Conference, Anchorage, Alaska. June 2019.

Publications*

1. Blomberg, E.J., and A. Ross. 2018. Research and management of spruce grouse along a southern range margin. The Wildlife Professional, Spring 2018.
2. Demography and population status of spruce grouse in northern Maine forests. Final Technical Report to Maine Outdoor Heritage Fund.

*Additional peer-reviewed publications are currently in prep.

Outreach

1. Presented a talk titled "Maine's upland game birds; new insights from research at the University of Maine" at the 80th Annual Eastern Maine Sportsman's Show, March 2018.
2. Delivered the opening keynote address at the 2018 Downeast Spring Birding Festival in Trescott, ME, May 2018, which included discussion of our ongoing spruce grouse research.

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