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Effects of forest characteristics on ruffed grouse nesting ecology in central Maine, USA

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Effective wildlife management requires a broad understanding of how forest structure and composition influence habitat use and vital rates during all aspects of species' life-cycles, however habitat characteristics may have variable importance during different life phases. Even though the ruffed grouse *Bonasa umbellus* is a popular game bird that has long been a focal species for management, a greater understanding of the links between forest characteristics and components of ruffed grouse reproduction would enhance managers' ability to promote the species. We monitored 45 nests belonging to 37 females during 2015–2017 in central Maine, USA, and evaluated the influence of forest characteristics on nest-site selection, nest survival and female survival while nesting. Ruffed grouse females selected nest sites with greater horizontal visual obstruction ($\beta = 0.16 \pm 0.06$ 85% CI) than found at other sites that were locally available to them, however this characteristic did not appear to improve nest survival or female survival while nesting. Cumulative nest success was 42.8% and daily nest survival was reduced when coarse woody debris (CWD) was present at nest sites ($\beta = -0.41 \pm 0.33$ 85% CI), but we found no evidence that other habitat characteristics or features of nests themselves were related to nest survival. However, reduced female survival while nesting was associated with presence of CWD ($\beta = -1.27 \pm 0.91$ 85% CI), greater tree basal area ($\beta = -0.96 \pm 0.81$ 85% CI) and greater conifer stem density ($\beta = -0.45 \pm 0.28$ 85% CI) at nest sites; females had a 74.4% chance of survival during the length of time required to successfully nest. Our results demonstrate the importance of forest characteristics on multiple components of species' nesting ecology, and we provided management suggestions to promote attractive ruffed grouse nesting habitat while potentially mitigating sources of nesting failure.

Keywords: *Bonasa umbellus*, composition, forest structure, habitat selection, nest survival, radio-telemetry

Species–habitat relationships are often complex (Morrison et al. 2012), therefore effective habitat management necessitates an understanding of the broad suite of characteristics required by a species throughout its annual cycle (Block and Brennan 1993). One common approach for obtaining this information is through resource selection studies, where resource use is compared to availability to identify habitat characteristics that are used more or less frequently than expected by chance (Johnson 1980, Sauder and Rachlow 2015). The key benefit of habitat, however, lies in its contribution to resource availability (e.g. access to food and protective cover), which in turn contributes to demographic success. For forest wildlife, population dynamics may be affected by vegetative structure and composition as

these characteristics have the potential to influence individual mortality risk (Todd et al. 2014, Gasperini et al. 2016) and reproductive success (Martin 1993, Streby and Andersen 2013). Importantly, habitat characteristics selected by avian species may have differential effects on individual vital rates, even within the same season (Chalfoun and Martin 2007). For example, greater cover can positively affect nest success by reducing the risk of nest predation (Martin and Roper 1988, Møller 1989), but the same nesting cover may also increase the mortality risk to the incubating adult by inhibiting their abilities to detect or escape predators (Wiebe and Martin 1998, Mönkkönen et al. 2007, Lima 2009). While animal populations are certainly influenced by other factors such as disease (Frick et al. 2010) and human harvest (Langvatn and Loison 1999), habitat manipulation is one action managers can take to enhance wildlife populations of interest. Consistent with the theory of adaptive habitat selection (Hildén 1965, Martin 1998), considering how a suite of habitat characteristics affects multiple vital rates in addition to habitat selection may aid in the development

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of habitat management guidelines that are based on links between habitat and its realized effects on populations (Mayor et al. 2009),

The ruffed grouse *Bonasa umbellus* is a resident galliform native to northern North America (Rusch et al. 2000), where it is an early-successional forest specialist (Dessecker and McAuley 2001). As a popular game bird, particularly in the central and eastern portions of its range (Rusch et al. 2000), the ruffed grouse has long been a species of interest to managers seeking to increase densities and improve sporting opportunities (Bump et al. 1947). Classic habitat management guidelines for this species were developed in forests dominated by aspen *Populus* spp., and have promoted heterogeneous forests created through patch clearcutting at relatively small scales. For aspen-dominated forests, adjacent patches 0.4–4.0 ha in size are clearcut in 10-year intervals under a 40-year rotation length (Gullion 1984), where rotation lengths may be modified to reflect the forest composition, site characteristics and management goals of specific areas or regions. The primary justification for these management strategies is the recognition that habitat requirements of ruffed grouse vary, particularly in regard to forest structure, throughout the annual life-cycle (Bump et al. 1947). While providing heterogeneous forested landscapes is a good general strategy for ruffed grouse habitat management (Kouffeld et al. 2013), there remains some uncertainty regarding how specific life stages (e.g. nest success, adult survival) are influenced by forest structure and composition, leaving room to build upon existing management targets.

Nesting is a crucial life phase for ruffed grouse because it represents the first major component of recruitment (Berner and Gysel 1969). Ruffed grouse are female-only, continuous incubators that may renest if their initial nesting attempt fails, but that raise only one brood of precocial young per year (Rusch et al. 2000). As ground-nesting birds, most ruffed grouse nests fail because eggs are destroyed by predators (Bump et al. 1947, Bergerud and Gratson 1988), however nests may also fail if the incubating female is killed by a predator while nesting (Lima 2009), if the nest is abandoned by the female (Ricklefs 1969, Pierce and Simons 1986), or because of weather-related events such as flooding (Sanders and Maloney 2002). Each of these outcomes may be influenced, in part, by characteristics of habitat at the nest site (Redmond et al. 1982, Moynahan et al. 2006). The process of nest-site selection is therefore critical for female ruffed grouse because they must select habitat characteristics based on their potential to reduce the likelihood of each possible source of failure (Martin 1998).

We studied nesting habitat ecology of radio-marked ruffed grouse females at two study areas in central Maine during springs 2015–2017. Our objectives were to 1) evaluate nesting habitat selection, to 2) quantify daily nest survival and cumulative nest success and to 3) assess female survival while nesting. We approached these objectives with an overarching goal of understanding how forest characteristics affected each component of ruffed grouse nesting ecology. We predicted that female ruffed grouse would select nest sites with habitat characteristics that improved their nest's likelihood of success and their own survival. To our knowledge this is the first ruffed grouse study to simultaneously assess effects of forest characteristics on multiple components of ruffed grouse nesting.

Material and methods

Study areas

Our first study area was in Waldo County, Maine, USA (44°47'97", 69°23'69"W) at Frye Mountain Wildlife Management Area (FM). This area was owned and managed by the Maine Department of Inland Fisheries and Wildlife, and was comprised of ~ 2100 ha of second-growth (i.e. harvested by humans at least once) upland forests that resulted from reforestation associated with widespread farm abandonment during the early 20th century. Northern hardwood tree species typically dominated forest stands on this landscape; maple *Acer* spp., birch *Betula* spp., white ash *Fraxinus americana*, quaking aspen *Populus tremuloides* and American beech *Fagus grandifolia* were the most frequently encountered deciduous species, and balsam fir *Abies balsamea* was the most common conifer. Frye Mountain was actively managed to promote habitat for ruffed grouse and other forest wildlife through small-scale clearcutting and mowing to maintain fields, and the rural landscape surrounding FM was predominantly maturing second-growth forest with private ownership, interspersed with small-scale agriculture.

Our second study area was in Penobscot and Hancock Counties, Maine, USA (44°98'47"N, 68°49'67"W), ~ 80 km northeast of FM, along a privately-maintained road known as the Stud Mill Road (SM). This area was comprised of expansive, privately-owned commercial forests, characterized by second-growth upland forest and wetlands. Common tree species at SM included balsam fir, maple, spruce *Picea* spp., birch, eastern white pine *Pinus strobus*, northern white cedar *Thuja occidentalis* and big-toothed aspen *Populus grandidentata*. Common avian predators at both study sites included red-tailed hawk *Buteo jamaicensis*, Cooper's hawk *Accipiter cooperii*, American crow *Corvus brachyrhynchos* and barred owl *Strix varia*. Common mammalian predators included red fox *Vulpes vulpes*, striped skunk *Mephitis mephitis*, raccoon *Procyon lotor*, coyote *Canis latrans*, American marten *Martes americana* and fisher *Pekania pennanti*. Additional details about each study area may be found in Mangelinckx et al. (2018), and see Davis et al. (2018) for a description of ruffed grouse hunting within each study area.

Field methods

Ruffed grouse monitoring

During August and September of 2014–2016, we captured and radio-marked ruffed grouse using methods described in Mangelinckx et al. (2018). We located and visually observed radio-marked females by homing to their locations at least twice weekly during the nesting seasons (late April to early July), 2015–2017. When we found a female in the same general area on consecutive visits, we flushed her to determine if she had a nest, and to record clutch size. We used egg flotation (McNew et al. 2009) to estimate incubation stage, and along with the average laying rate and incubation period of ruffed grouse (Rusch et al. 2000), we estimated initiation and predicted the hatch dates for each nest. We classified nests as first nests or renests based on each female's known nesting history for the year, or in a few cases using clutch size and timing within the nesting season (four renests were

identified using this method). We checked all nests for activity (i.e. presence of the female) twice weekly by circling incubating females from ≥ 15 m away. When a female left her nest, we inspected the contents of the nest bowl to determine the nest's fate, either success (≥ 1 eggs hatched) or failure (0 eggs hatched), based on the condition of eggshell remains. We implemented several precautionary measures to limit the introduction of our scent to nest sites, including wearing knee-high rubber boots when we approached suspected or known nests, and wearing rubber gloves whenever we touched nest-bowl contents. We also avoided kneeling in the immediate vicinity of the nest, and attempted to minimize trampling of vegetation.

Habitat sampling

Within three days after a nest's predicted or actual hatch date (depending on whether it failed or hatched, respectively), we sampled habitat characteristics at nests and two random locations located between 50 m and 200 m from each nest. We chose to sample habitat characteristics for failed nests on the predicted hatch date, rather than at nest fate, to avoid biases associated with the inherent confounding between plant growth and timing of nest fate (Gibson et al. 2016). The first random location was obtained using a randomly-chosen azimuth (i.e. compass direction), and the second was located 90° to the first azimuth to ensure separation between random locations. We used a lower distance limit of 50 m to ensure independence between nests and random locations, and the upper distance limit of 200 m to be consistent with Small and Rusch's (1989) estimate for the mean daily movements of female ruffed grouse during the spring. In doing so we assumed locations ≤ 200 m from nests represented potential nest sites that were available to individual females prior to egg laying; thus, this distance was most consistent with Johnson's (1980) 3rd order (i.e. within home range) of habitat selection. If random locations occurred in non-forest, we moved plot centers into the closest forest cover, which we defined as an area with more or less continuous cover of woody stems taller than breast height. We did this because we assumed habitat availability for ruffed grouse nests was constrained by presence of forest cover, which is selected by the species at a higher order of selection (Johnson 1980). We centered sampling plots on the nest bowl, whereas plot centers of random locations were placed adjacent to the nearest tree, stump or log (i.e. the closest plausible nest site; Bump et al. 1947) that could presumably act as a nest location. This step was necessary to accurately assess nest-site

availability because ruffed grouse usually place their nests against these objects (Bergerud and Gratson 1988), therefore not doing so could bias aspects of our habitat sampling.

Based on existing literature, we selected six habitat characteristics to represent hypotheses about resources that were potentially important to ruffed grouse females when selecting nest sites, and/or that may contribute to nest success or female survival while nesting (Table 1). We investigated the potential influence of the density of seedlings and saplings > 1 m tall and < 10 cm diameter at breast height (dbh; hereafter, stem density) given the centrality of this habitat characteristic within guidelines for ruffed grouse habitat management (Gullion 1984, Dessecker and McAuley 2001). We also investigated the effects of stem species class (i.e. deciduous versus conifer), as there is some disagreement in the literature regarding the value of conifer stems as components of ruffed grouse habitat; some studies have suggested conifers as a necessary habitat component (Bump et al. 1947, Chambers and Sharp 1958), while others have suggested that conifers are generally detrimental to ruffed grouse (Gullion 1984, Zimmerman et al. 2009). We evaluated total basal area (m^2ha^{-1}) and conifer basal area (m^2ha^{-1}); besides being generally good descriptive metrics of forest structure, we were specifically interested in basal area because one study in the central Appalachians found that female ruffed grouse selected sites with greater basal area for nesting, and that it was positively related to nest success (Tirpak et al. 2006). We also estimated percent ground cover by forbs, seedlings, *Rubus*, ferns and coarse woody debris (CWD; dead woody vegetation ≥ 10 cm in diameter) using the percent cover delineations specified by Daubenmire (1959). We investigated the potential role of CWD (presence/absence) in ruffed grouse nesting ecology, because Tirpak et al. (2006) also observed a positive association of this habitat characteristic to nest-site selection and nest success. Lastly, we assessed horizontal visual obstruction (%) to assess the degree to which individual ruffed grouse nests were visually concealed from predators (Martin and Roper 1988, Møller 1989). Because little research had focused on ruffed grouse nesting ecology in Maine, we recorded each nest's substrate (e.g. tree, stump, log, etc.) to document potential regionally-specific substrate use that may be different from patterns observed in other geographic regions.

While we were primarily interested in examining the effects of forest characteristics, we hypothesized that weather conditions and proximity to roads and trails (Gates and Gysel 1978, Tirpak et al. 2006) may influence ruffed grouse

Table 1. Descriptions of habitat covariates included in all analyses.

Covariate	Description
Total stem density (stems ha^{-1})	All woody stems < 10 -cm dbh within two perpendicular 20×2 m belt transects centered on point center*
Conifer stem density (stems ha^{-1})	Conifer stems < 10 -cm dbh within two perpendicular 20×2 m belt transects centered on point center
Total basal area (m^2ha^{-1})	All trees 'in' using a 10-factor wedge prism as seen from point center
Conifer basal area (m^2ha^{-1})	All conifers 'in' using a 10-factor wedge prism as seen from point center
Coarse woody debris	Presence/absence of coarse woody debris (i.e. deadwood ≥ 10 -cm in diameter) within four Daubenmire frames oriented 3 m from point center, and one centered on point center
Horizontal visual obstruction (%)	Average obstruction of four readings of a 25×25 cm coverboard placed at point center

* Point center for nest locations is the nest bowl, while point center at random locations was the nearest plausible nest site to the random coordinates.

nesting success. We therefore included these variables in our models to examine the relative importance of forest characteristics and avoid potentially confounding effects of weather and proximity to roads. We obtained daily precipitation (mm), daily maximum temperature (°C) and daily minimum temperature (°C) measurements for each nesting season from NOAA operated weather stations in Old Town, Maine (44°92'81"N, 68°70'06"W) and Belfast, Maine (44°43'95"N, 68°98'92"W), corresponding to weather at SM and FM, respectively. We measured the distance (m) between each nest and the nearest linear feature (i.e. roads and all-terrain vehicle trails) using Google Earth (<google.com/earth/>).

Analytical methods

Nest-site selection

We evaluated ruffed grouse nest-site selection using resource selection functions (RSFs) that took the form of generalized linear models (GLMs; Nelder and Wedderburn 1972) constructed in program R (<www.r-project.org>). In this analysis, we compared all nest sites to our sample of available nest sites (i.e. random locations). To assess whether it was appropriate to include two nests from the same female in our analyses (we found no more than two nests per individual female during our study), we computed correlations for all variables for nests that were sampled from females repeatedly (i.e. a pairwise comparison of measures from first and second nests for each variable). We found no significant correlation between habitat measures ($r = |0.03| - |0.39|$), and therefore concluded that including two nests from a given female did not introduce bias associated with repeated sampling. Because percent ground cover by CWD was zero-inflated, we converted CWD into a binary covariate that represented its presence or absence at a nest site for use in this and all subsequent analyses. Prior to constructing models, we Z-standardized all covariates and investigated the potential for high correlations (Pearson's correlation $|r| \geq |0.60|$) among them; no pairs of covariates were highly correlated. We then created a series of univariate models where the effect of each covariate on nest-site selection was compared to a null model. We considered a model supported when its Akaike's information criterion score adjusted for small sample size (AICc) was lower than or within 2.0 Δ AICc of the null model, and covariates supported when beta estimates and 85% confidence intervals (CIs; Arnold 2010) did not overlap zero. We included all supported covariates in a final additive model and considered the AICc score of this model in comparison to all univariate models. Using the final model, we evaluated the biological importance of each habitat characteristic by interpreting the magnitude and direction of its beta coefficient.

Nest and nesting female survival

We estimated daily nest survival for the combined egg laying and incubation periods using nest survival models in program MARK (White and Burnham 1999) and constructed in program R using the package 'RMark' (Laake 2013). We used a two-step model building approach to identify covariate support. In step 1, we evaluated the effects of the ten Z-standardized covariates on nest survival, including the six

habitat covariates (Table 1), distance to linear feature, and three time-varying weather covariates that corresponded with each day of the nesting season. In addition, we assessed systematic temporal trends (linear and quadratic) in nest survival based on day of the nesting season, and whether there were differences in survival between first nests and renests, female age classes (females in their third year of life or later versus females in their second year of life), years (2015, 2016, 2017) and study areas (FM versus SM). We evaluated support for each model using the previously described criteria, then in step 2, we combined all supported covariates into a final additive model and compared AICc metrics from this final model to all others. We interpreted beta coefficients from the final model to make inferences regarding covariates that affected ruffed grouse nest survival. We estimated cumulative nest success (i.e. the probability a nest will hatch ≥ 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. We calculated standard errors of cumulative survival rates using the delta method (Powell 2007) within the program R package 'emdbook' (Bolker 2016).

We then assessed whether this same set of covariates contributed to the survival of females while 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, such that each female was alive and available for death until the fate of their nests. Female survival in this context therefore 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 different factors influencing the mortality risk of nesting females compared with the fate of the nest in general. Hence, the interpretation of these results was based solely on whether the covariates we investigated caused variation in female survival while nesting, a specific source of nesting failure.

Lastly, we attempted to disentangle factors affecting female survival while nesting from those influencing other sources of nesting failure (e.g. predators consuming eggs). To do this, we followed a similar analysis to our assessment of female mortality, where we right censored all nests where the incubating female was killed during nesting; thus these nests were considered active and available for failure until the day when the female was killed. This allowed us to evaluate how the covariates contributed to sources of nesting failure that were explicitly not associated with female mortality during nesting.

To illustrate that our approach for evaluating covariate support based on univariate models was robust, we conducted three auxiliary analyses wherein we ran all combinations of 1, 2 and 3 variables for each survival analysis. This included all plausible combination of variables that may have been considered, but without constructing models that were too complex given our sample sizes. For each analysis, the top-ranked model among the hundreds we considered (> 600 models in each analysis) was identical to the final additive model structures we arrived at using our simpler univariate approach, which required only 18 models per analysis. This demonstrates that results from our two-step approach to model building are empirically sound.

Results

We monitored survival and measured habitat characteristics at 45 nests ($n_{2015}=16$, $n_{2016}=17$, $n_{2017}=12$), belonging to 37 individual ruffed grouse, of which 34 were radio-marked females and three were unmarked females whose nests we found opportunistically. No females were monitored during more than one nesting season, and the maximum number of nests for any individual was 2. The average initiation date for first nests ($n=32$) was April 28 (± 4.0 SD) and the average hatch date was June 4 (± 3.5 SD; $n=15$), whereas average renests ($n=13$) were initiated on May 24 (± 8.1 SD) and hatched on June 27 (± 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 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 second or later nesting season was $9.95 (\pm 0.94$ SD) compared to $9.56 (\pm 1.51$ SD) for females in their first nesting season. The average clutch size of renests for females in their second or later nesting season was $7.11 (\pm 1.05$ SD), and we observed only two renests belonging to females in their first nesting season, each with eight eggs.

Nest-site selection

Of 45 nests, 22 (49%) were adjacent to live trees ≥ 10 -cm dbh, 9 (20%) were positioned against seedlings or saplings < 10 -cm dbh, 6 (13%) were under logs or in brush piles, four (9%) were adjacent to snags or stumps and four (9%) were in thick understory vegetation (i.e. ferns or bramble), but not adjacent to any larger object. We did not observe any nests adjacent to rocks or boulders. Two of the six habitat covariates performed better than the null model according to AICc (Table 2) and had 85% CIs that did not overlap zero. When combined for the final additive model, we found that nesting females selected nest sites with greater horizontal visual obstruction ($\beta=0.16 \pm 0.06$ 85% CI; Fig. 1). Selection of conifer stem density was not supported in the final model (85% CI included 0.0). We combined measurements of percent ground cover by seedlings, forbs, *Rubus* and ferns

Table 2. Model selection results from generalized linear models comparing nest sites used by ruffed grouse ($n=45$) to randomly chosen locations available as nest sites ($n=90$) at two study areas in central Maine, USA, 2015–2017. Delta AICc is the difference in AICc from the top model, Wi is the model weight and K is the number of model parameters.

Model	AICc	Δ AICc	Wi	K
Horizontal visual obstruction	170.55	0.00	0.50	2
Full model ^a	170.60	0.06	0.49	3
Conifer stem density	179.67	9.12	0.01	2
NULL	182.15	11.61	0.00	1
Coarse woody debris	183.03	12.48	0.00	2
Conifer basal area	183.84	13.30	0.00	2
Basal area	183.95	13.40	0.00	2
Total stem density	183.96	13.42	0.00	2

^a Full model=Horizontal visual obstruction+Conifer stem density.

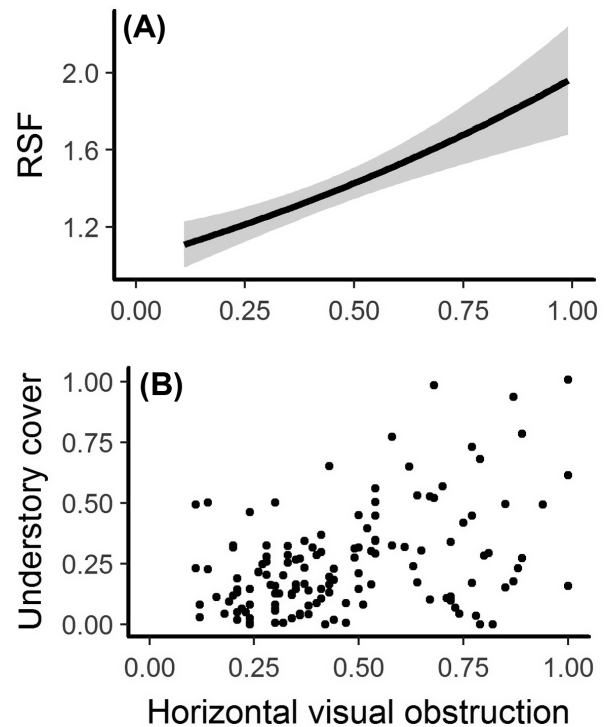


Figure 1. (A) Relationship between horizontal visual obstruction and relative selection of nest sites compared to locally available random locations (resource selection function; RSF), shown with 85% CIs represented by gray ribbon. RSF reflects an exponential form of a resource selection probability function (RSPF) which does not constrain model predictions to be bounded between 0.0 and 1.0. (B) Relationship between horizontal visual obstruction and understory cover (i.e. proportion of ground covered by forbs, *Rubus*, ferns and seedlings combined; $r=0.43$). Data were collected at two study areas in central Maine, USA, during springs 2015–2017.

to evaluate whether these variables were collective determinants of visual obstruction, and we observed a moderate correlation with horizontal visual obstruction ($r=0.43$; Fig. 1). We did not detect selection or avoidance of the other habitat variables (Table 2).

Nest survival

We censored one nest from our survival analysis that was abandoned immediately after we flushed the female. Of the remaining 44 nests, 24 were successful and 20 failed. Twelve nests (60% of failures) were destroyed by predators, where four nests had eggshell fragments in or around the nest bowl and eight had no eggshell 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. The mean daily survival rate for all nests over the course of our study was $0.9763 (\pm 0.0052$ SE), resulting in cumulative nest success of $0.43 (\pm 0.08$ SE).

Two of the covariates performed better than the null model according to AICc, however only one met fully our criteria for support (Table 3). We found that nests with CWD near the nest bowl experienced lower success than

Table 3. Model selection results for daily nest survival of ruffed grouse ($n=44$) at two study areas in central Maine, USA, 2015–2017. Delta AICc is the difference in AICc from the top model, Wi is the model weight and K is the number of model parameters.

Model	AICc	Δ AICc	Wi	K
Full model ^a	147.54	0.00	0.15	2
Initiation date	148.61	1.07	0.09	2
NULL	148.79	1.24	0.08	1
Renest	149.01	1.47	0.07	2
Conifer stem density	149.44	1.78	0.06	2
Basal area	149.50	1.95	0.06	2
Time trend	149.53	1.98	0.06	2
Time trend quadratic	149.85	2.30	0.05	3
Distance to linear feature	149.91	2.37	0.05	2
Horizontal visual obstruction	149.96	2.41	0.05	2
Year	149.99	2.45	0.05	2
Female age	150.12	2.57	0.04	2
Maximum daily temperature	150.46	2.91	0.04	2
Total stem density	150.54	2.99	0.03	2
Minimum daily temperature	150.71	3.16	0.03	2
Precipitation	150.75	3.20	0.03	2
Conifer basal area	150.77	3.22	0.03	2
Study area	150.79	3.25	0.03	2

^a Full model=Coarse woody debris.

those without CWD nearby ($\beta = -0.41 \pm 0.33$ 85% CI), resulting in cumulative probabilities of success of 0.30 (± 0.10 SE) and 0.44 (± 0.09 SE; Fig. 2), respectively. Nest initiation date was not supported because its 85% CIs overlapped zero. We found no evidence that daily nest survival was affected by the other habitat covariates or any of the other variables tested.

Nesting female survival

We monitored female survival during 43 nesting attempts, excluding two nesting attempts of unmarked females where we could not determine female status after nest loss. Six females were killed by predators during incubation of a first nest and one was killed during incubation of a renest. Four of these mortalities occurred in 2015, three occurred in 2016 and no mortalities occurred in 2017. The mean daily survival rate of females while nesting was 0.9916 (± 0.0032 SE), which equated to a 0.74 (± 0.05 SE) probability that a female ruffed grouse survived a single nesting attempt for the duration of the laying and incubation. Three of the covariates we investigated met our requirements for inclusion in the final additive model (Table 4). From the final model, we found evidence that basal area, conifer stem density and the presence of CWD were associated with the survival of females while nesting. Female survival while nesting was negatively associated with greater basal area ($\beta = -0.78 \pm 0.61$ 85% CI) and greater conifer stem density ($\beta = -0.41 \pm 0.25$ 85% CI; Fig. 2) at nest sites, where a 9.3 m² ha⁻¹ (i.e. a one standard deviation) increase in basal area and a 3454 stems ha⁻¹ increase in conifer stem density was associated with 13.6% and 7.4% reduction in female survival, respectively. In addition, females whose nests had CWD nearby were ~ 25% less likely to survive compared to females whose nest sites were without CWD ($\beta = -1.12 \pm 0.81$ 85% CI; Fig. 2). We found

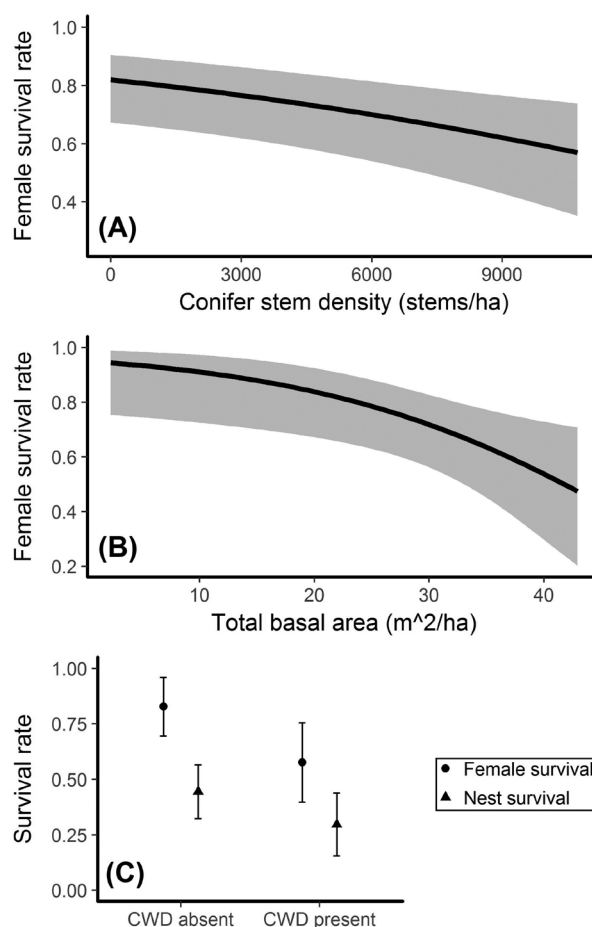


Figure 2. Effects of (A) conifer stem density (conifer stems < 10 cm dbh ha⁻¹) and (B) total basal area (m² ha⁻¹) on female survival while nesting. Effects of the (C) presence of coarse woody debris (CWD) near nests on ruffed grouse nest survival and survival of ruffed grouse females while nesting. Relationships are depicted using coefficients from the best supported models describing variation in nest survival and female survival while nesting. Data were collected at two study areas in central Maine, USA, during springs 2015–2017. Gray ribbons represent 85% CIs and error bars represent standard errors.

no evidence that female survival while nesting was affected by other habitat covariates or any other covariates tested.

Nest survival without female mortality

When nests where the incubating female was killed were censored from the nest survival analysis, we found no evidence that any covariates caused variation in other sources of nesting failure (Table 5). While many covariates were within 2.0 Δ AICc of the null model, the 85% CIs of each overlapped zero.

Discussion

We found that females exhibited the strongest selection for nest sites with increased horizontal visual obstruction. The component features of the forest understory that we measured (seedlings, forbs, *Rubus*, ferns) each contributed to this visual obstruction, but there was not a single understory

Table 4. Model selection results for daily survival of nesting females (n=43) at two study areas in central Maine, USA, during nesting seasons 2015–2017. Daily survival was estimated using nest survival models in Program MARK. Delta AICc is the difference in AICc from the top model, Wi is the model weight and K is the number of model parameters.

Model	AICc	ΔAICc	Wi	K
Full model ^a	64.32	0.00	0.56	4
Coarse woody debris	66.72	2.40	0.17	2
Basal area	69.43	5.10	0.04	2
Conifer stem density	69.63	5.31	0.04	2
NULL	70.64	6.32	0.02	1
Distance to linear feature	71.00	6.67	0.02	2
Time trend quadratic	71.26	6.94	0.02	3
Renest	71.27	6.95	0.02	2
Total stem density	71.30	6.97	0.02	2
Horizontal visual obstruction	71.74	7.41	0.01	2
Conifer basal area	71.89	7.57	0.01	2
Nest initiation date	71.90	7.57	0.01	2
Maximum daily temperature	72.32	8.00	0.01	2
Time trend	72.33	8.01	0.01	2
Minimum daily temperature	72.59	8.27	0.01	2
Nesting female age	72.63	8.31	0.01	2
Study area	72.64	8.32	0.01	2
Precipitation	72.65	8.32	0.01	2

^a Full model=Coarse woody debris+Basal area+Conifer stem density.

feature that drove the relationship. A variety of woody and herbaceous plant types are therefore likely to provide this habitat characteristic, and selection of horizontal visual obstruction indicates that the understory is perhaps a previously undervalued component of ruffed grouse nesting habitat. Traditional ruffed grouse habitat management suggested that stands with dense midstories are optimal for ruffed grouse nesting because such areas inhibit the growth of an understory (Gullion 1984, Thompson et al. 1987), which was thought to be unnecessary for nesting given the concealment provided by the cryptic coloration of females (Bergerud and Gratson 1988). Other studies have supported this claim by showing no effect of nest concealment on either ruffed grouse nest-site selection or nest success (Larson et al. 2003, Tirpak et al. 2006), however another study observed greater nesting success in areas with dense understories (Maxson 1978). Although we observed selection of horizontal visual obstruction, this characteristic did not appear to benefit females by increasing their nest success. Females may select nest sites with well-developed understory vegetation to promote subsequent components of reproduction, such as brood-rearing. Understory vegetation likely contributes to chick survival and growth by providing important food resources such as invertebrates and low-growing forbs (Kimmel and Samuel 1984). The area immediately surrounding the nest site is the first habitat that will be encountered by a female’s precocial, self-feeding young and females may therefore consider the proximity to chick food resources when deciding where to nest. This pattern has been observed in other avian species (Streby et al. 2014), and female ruffed grouse in our system selected brood rearing habitat with greater availability of forbs and *Rubus* (Mangelinckx et al.

Table 5. Model selection results for daily nest survival of ruffed grouse (n=44) at two study areas in central Maine, USA, 2015–2017. Nests where the incubating female was killed by predators were right censored from the analysis, therefore this analysis relates only to other sources of nesting failure (n_{predation} = 12, n_{abandonment} = 1). Delta AICc is the difference in AICc from the top model, Wi is the model weight and K is the number of model parameters.

Model	AICc	ΔAICc	Wi	K
NULL	106.17	0.00	0.12	1
Initiation date	106.74	0.57	0.09	2
Maximum daily temperature	107.00	0.84	0.08	2
Time trend	107.17	1.00	0.07	2
Female age	107.31	1.15	0.07	2
Renest	107.52	1.35	0.06	2
Conifer basal area	107.88	1.72	0.05	2
Coarse woody debris	108.01	1.84	0.05	2
Horizontal visual obstruction	108.01	1.85	0.05	2
Total stem density	108.03	1.87	0.05	2
Precipitation	108.09	1.92	0.05	2
Study area	108.13	1.97	0.04	2
Minimum daily temperature	108.14	1.97	0.04	2
Distance to linear feature	108.17	2.01	0.04	2
Conifer stem density	108.17	2.01	0.04	2
Basal area	108.18	2.01	0.04	2
Time trend quadratic	108.99	2.82	0.03	3
Year	109.33	3.17	0.03	3

2018). Regardless of mechanism, considering the role of the forest understory to ruffed grouse nesting ecology is clearly important because females chose to nest in areas with greater understory concealment.

We found that all habitat variables supported in our demographic analyses (i.e. CWD, conifer stem density and basal area) were associated with female mortality during nesting, while there was limited to no support for habitat effects on other sources of nest failure (primarily consumption of eggs by predators). These results may suggest that predation of ruffed grouse clutches occurred more randomly and was carried out by generalist predators that detected nests opportunistically. In our study area, this includes mammalian meso-carnivores such as red fox, striped skunk and raccoon. A previous study of two sympatric forest grouse (capercaillie *Tetrao urogallus* and black grouse *Tetrao tetrix*) in Norway found that mammalian predators were not more likely to locate grouse nests with increased search effort (Storaas et al. 1999), supporting the assertion that predation of nests belonging to forest grouse is a chance event. If indeed predation of forest grouse nests is a random process, then rates of nest predation may be a function of landscape configuration, predator density or other factors that are not explicitly associated with the nest micro-site (Whittingham and Evans 2004, Baines et al. 2016). In particular, fragmentation likely influences the community dynamics of generalist predators because these species are known to select small habitat patches and edges (Cervinka et al. 2011). Therefore, a thorough understanding of an area’s predator community and how it is influenced by a site’s spatial configuration is necessary to guide effective management to reduce predation of forest grouse nests. In contrast, we found that specific habitat features (i.e. areas with greater basal area, conifer stem

densities and CWD present) were associated with the probability that a female would be killed by a predator, suggesting a stronger link between local habitat characteristics at nests sites and female mortality risk and perhaps a greater association with specialist predators (e.g. *Accipiter* hawks). For example, the northern goshawk *Accipiter gentilis* is a specialist predator of forest grouse in Europe (Tornberg 2001) and North America (Hewitt et al. 2001) that is known to select specific forest characteristics for foraging (Beier and Drennan 1997). Such characteristics presumably increase predatory foraging efficiency via associations with alternate prey abundance (e.g. CWD and small mammals; Fauteux et al. 2012) and/or hunting success (Andruskiw et al. 2008). Nevertheless, based on our results, land managers may be able to reduce the predation risk to incubating forest grouse females through habitat management.

Female ruffed grouse neither selected nor avoided areas for nesting that contained CWD, yet its presence in the immediate vicinity of the nest reduced overall nest success via its negative effect on female survival. We recognize that CWD is an important habitat component for breeding males, because males most often use fallen logs as platforms for their drumming displays (Zimmerman and Gutiérrez 2008, Davis 2017). However, Roy et al. (2015) observed relatively broad distribution and high densities of drumming males in a system where limited CWD was present, which suggests that drumming platforms are not likely to limit components of ruffed grouse habitat. This allows managers some flexibility to promote survival and reproductive success during nesting without necessarily compromising a habitat feature that is a requirement of other life-stages. We also acknowledge that in our system CWD was often completely absent from nest sites, which required us to treat it as a binary (present/absent) variable in our analysis. Understanding how variation in CWD density affects ruffed grouse nesting could provide more nuanced insights, but was not possible from our analysis.

Our results suggest that greater conifer stem densities at nest sites were associated with reduced female survival while nesting. Davis (2017) found that male ruffed grouse selected display locations with greater conifer stem density, and both Berkeley and Gutiérrez (2017) and Davis (2017) showed no effect of conifer use on male display behaviors. Other previous studies observed either limited (< 5%; Bump et al. 1947, Maxson 1978) or more frequent use (> 33%; Larson et al. 2003) of conifer cover types, but said little regarding their possible effects on vital rates. Thus, the role of conifers in affecting ruffed grouse demographics as a whole remains unclear, but during our study it played a negative role in female survival during nesting.

We found no evidence that weather affected ruffed grouse nest success or female survival, despite multiple plausible mechanisms that could cause such effects. Ambient temperature, both daily maximum and daily minimum, can profoundly influence the activity patterns (Conway and Martin 2000) and energetics (Kern et al. 1993) of incubating birds, thus increasing the chance of nest detection by visual predators (Coates and Delehanty 2008). Predation risk may also be exacerbated by precipitation, because moisture enhances odorants and may increase the detectability of nests by olfactory predators (Conover 2007). Multiple

studies of wild turkey *Meleagris gallopavo*, a galliform that co-occurs with ruffed grouse in portions of its range, observed increased nest predation during wet weather (Palmer et al. 1993, Roberts et al. 1995). However, few ruffed grouse studies have considered weather as a possible factor influencing nest success. Bump et al. (1947) qualitatively commented that weather had 'no recognizable effect' on the success of > 1500 ruffed grouse nests in New York, and Maxson (1977) observed altered activity patterns by incubating females when it was raining, but did not comment on resulting effects on nest success. While we did not observe an effect of weather on nest survival, it is widely believed that weather can affect the survival of grouse chicks. Cold, wet weather may induce hypothermia if chicks get wet, or malnutrition when chicks need to be brooded longer to maintain body temperatures, thus losing time that would otherwise be spent feeding (Erikstad and Andersen 1983, Flanders-Wanner et al. 2004, Gregg and Crawford 2009). Therefore, weather may still have an effect on ruffed grouse reproductive success by decreasing chick survival, but our results suggest that it did not affect nest success or the survival of nesting females during our study.

We found that nesting female ruffed grouse during in our study had a > 25% chance of being killed by a predator before they could successfully hatch a clutch of eggs. While we observed a relatively modest number of mortalities, this level of mortality is, to our knowledge, unprecedented in the ruffed grouse literature. Maxson (1978) and Small et al. (1996) each observed a single nesting female killed by predators, representing 6.7% and 4.3% of their samples, respectively, and Larson et al. (2003) observed two (5.0%) nesting female mortalities. Other forest grouse species have been found to experience greater female mortality during nesting; a study of spruce grouse *Falcipennis canadensis* productivity in Maine observed mortalities for 26% of their sample of radio-marked females (Whitcomb et al. 1996). When we compare the survival of nesting females during our study to spring survival of the population as a whole (Davis et al. 2018), the mortality of females on nests (28.4%) was considerably higher than the background mortality occurring in the population at the same time (~10%), and was unlikely to have occurred based on chance alone. This indicates that nesting was a particularly risky activity for ruffed grouse females in our system, likely because of increased vulnerability to predators while associated with a nest.

Conclusions

Contrary to ruffed grouse studies in other regions, our results suggest that dense understories are a desirable component of ruffed grouse nesting habitat based on their strong selection for this characteristic. Because we did not observe an effect of understory cover on nest success or female survival while nesting, it may be selected at nest sites to benefit chicks immediately after hatch through the food resources it provides. We also found that increased conifer stem density and basal area were associated with reduced female survival while nesting. Therefore, we recommend that managers maintain conifer stem densities < 4000 stems ha⁻¹ and basal areas < 24 m² ha⁻¹ to promote female survival (Fig. 2). In addition,

we found that the presence of CWD in proximity to the nest bowl was associated with reduced overall nest success via its association with female mortality while nesting. As CWD is not likely a limiting resource for ruffed grouse males that use fallen logs as display platforms, we propose that managers exhibit caution when retaining CWD during timber harvests for the benefit of ruffed grouse because this resource may limit ruffed grouse females' abilities to survive while nesting and ultimately achieve reproductive success.

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