# **Ruffed grouse brood habitat selection at multiple scales in Pennsylvania: implications for survival**

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**Abstract:** Declines in ruffed grouse (*Bonasa umbellus* (L., 1766)) populations in the central and southern Appalachians may be linked to low brood survival. Therefore, managing for high-quality brood habitat could improve grouse numbers. Understanding how brood habitat selection affects survival and the spatial scale at which this occurs is therefore fundamental to developing effective habitat management strategies. From 1999–2002, we monitored 38 broods for 5 weeks post hatch and estimated utilization distributions (n = 28), site-scale habitat use (n = 21), and daily survival rate (mean = 0.966, range = 0.920–0.997, and n = 19). Relative to available habitat, broods selected sites with greater herbaceous ground cover and higher small (<2.5 cm diameter at breast height, DBH) stem densities and landscapes containing higher proportions of road and young deciduous forest. Herbaceous ground cover provided arthropod prey and concealment from predators and was a primary factor driving habitat selection. High stem densities and early successional habitats provided increased security, but were only used if adequate ground cover was present. Broods strongly selected roads and experienced higher survival near edges. However, higher road densities were associated with lower survival at the landscape scale. This pattern reflects the differential scale at which grouse and their predators respond to edge.

**Résumé :** Le déclin des populations de gélinottes huppées (*Bonasa umbellus* (L., 1766)) dans le centre et le sud des Appalaches peut être relié à la faible survie des couvées. Un aménagement qui favoriserait les habitats de haute qualité pour les couvées pourrait améliorer les densités de gélinottes. Pour mettre au point des stratégies efficaces de l'aménagement de l'habitat, il est donc nécessaire de comprendre comment la sélection de l'habitat affecte la survie de la couvée et de connaître l'échelle spatiale à laquelle cela se produit. De 1999 à 2002, nous avons suivi 38 couvées pendant cinq semaines après l'éclosion et estimé la répartition de l'utilisation (n = 28), l'emploi de l'habitat à l'échelle du site (n = 21) et le taux quotidien de survie (moyenne = 0,966, étendue = 0,920–0,997 et n = 19). Relativement à l'habitat disponible, les couvées choisissent des sites qui ont une couverture herbacée du sol plus importante et des densités plus fortes de petites tiges (<2,5 cm de diamètre à hauteur de poitrine, DBH), ainsi que des paysages contenant de plus fortes proportions de routes et de jeunes forêts décidues. La couverture herbacée au sol fournit des arthropodes comme proies ainsi qu'un abri contre les prédateurs et elle est un des facteurs principaux qui déterminent le choix de l'habitat. Une forte densité de tiges et des habitats du début de la succession procurent une sécurité accrue, mais ces milieux ne sont utilisés que s'il y a une couverte végétale adéquate au sol. Les couvées font une sélection très positive des routes et ils bénéficient d'une meilleure survie près des lisières. Cependant, les densités plus fortes de routes sont associés à une survie réduite à l'échelle du paysage. Ce patron illustre les différences d'échelles auxquelles les gélinottes et leurs prédateurs réagissent aux lisières.

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# Introduction

Ruffed grouse (hereinafter grouse) (*Bonasa umbellus*, (L. 1766)) populations in the central and southern Appalachians have historically occurred at lower densities than those in

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<sup>1</sup>Corresponding author (e-mail: john\_tirpak@fws.gov). <sup>2</sup>Present address: Lower Mississippi Valley Joint Venture, US Fish and Wildlife Service, Vicksburg, MS 39180, USA. more central portions of the species' geographic range (Servello and Kirkpatrick 1989). Nevertheless, continued declines in both grouse numbers (Butcher and Niven 2007) and their preferred early successional forest habitats (Trani et al. 2001) have raised concern for this species' long-term status. Research on grouse in the central and southern Appalachians indicates growth of the populations in this region is most sensitive to changes in brood survival (Tirpak et al. 2006; Devers et al. 2007). Thus, management efforts focused on improving this demographic parameter are likely to provide the most effective strategy for ultimately increasing grouse numbers. One potential mechanism for enhancing brood survival is improving the quality of brood habitat. However, this requires not only an understanding of brood habitat selection but also an explicit consideration for the fitness consequences of habitat selection (i.e., the influence of brood habitat characteristics on survival; DeSante and Rosenberg 1998; Jones 2001).

Brood habitat selection is driven primarily by the constraints imposed on grouse by their developmental life history. Grouse chicks are precocial and leave the nest in search of food almost immediately after hatching. During their first few weeks, broods rely heavily on a diet of proteinrich arthropods and seek habitats with dense herbaceous ground cover that support an ample supply of insect prey (Hollifield and Dimmick 1995; Haulton et al. 2003). This preference for dense ground vegetation, particularly on mesic sites, has been well-documented and is an almost ubiquitous characteristic of brood habitat across the entire range (Stewart 1956; Sharp 1963; Berner and Gysel 1969; Porath and Vohs 1972; Stauffer and Peterson 1985; Thompson et al. 1987). Nevertheless, food availability is not the only factor affecting brood habitat quality. Predation is a major cause of chick mortality, especially within the first 5 weeks post hatch (Larson et al. 2001; Smith 2006). Therefore, factors that influence the ability of broods to elude predators may affect survival rates. Ground vegetation, small stem density, and coarse woody debris may provide escape cover and conceal broods from detection or capture by potential predators (Godfrey 1975; Rogers and Samuel 1984; Giroux et al. 2007).

Factors at the landscape scale may also play a critical role in determining habitat use by broods. Grouse broods utilize a wide variety of habitat types, including regenerating forests, logging roads, forest edges, mature forest understories, alder thickets, reclaimed surface mines, and wildlife clearings (Stewart 1956; Porath and Vohs 1972; Kimmel and Samuel 1978; Godfrey 1975; Stauffer and Peterson 1985; Scott et al. 1998; Haulton et al. 2003). However, they avoid evergreen forest stands and large openings and clearings (Porath and Vohs 1972; Godfrey 1975), potentially in response to higher predator abundance or unfavorable microclimates in these habitats (Gullion and Marshall 1968; Rusch and Keith 1971; Kimmel and Samuel 1984). Brood survival may also be influenced by factors operating at the landscape scale as predator abundance is affected most strongly by conditions above the site scale (Chalfoun et al. 2002). Therefore, management focused solely on provisioning the appropriate habitat conditions at the site scale may have lower returns than anticipated if applied within an inappropriate landscape context. Consequently, our objectives were to (i) quantify grouse brood survival, (ii) assess brood habitat selection at the site and landscape scales, and (iii) identify habitat characteristics associated with brood survival at these scales.

### Materials and methods

We conducted this study on a 2000 ha tract of the Moshannon State Forest, approximately 15 km north of Clearfield, Pennsylvania. The site was primarily forested but interspersed with small roads, clearings, and utility rightsof-way. Mature forest stands (~500 ha) were comprised mainly of oaks (Quercus spp. L.) and northern hardwoods (American beech (Fagus grandifolia Ehrh.), birch (Betula spp. L.), and maples (Acer spp. L.), while regenerating pin cherry (Prunus pensylvanica L. f.) and aspen (both Populus tremuloides Michx. and Populus grandidentata Michx.) dominated the remaining 1500 ha area that was impacted by a 1985 tornado. Potential predators of juvenile grouse on the area included Cooper's hawk (Accipiter cooperii (Bonaparte, 1828)), sharp-shinned hawk (Accipiter striatus Vieillot, 1808), northern goshawk (Accipiter gentilis (L., 1758)), redtailed hawk (Buteo jamaicensis (J.F. Gmelin, 1788)), redshouldered hawk (*Buteo lineatus* (J.F. Gmelin, 1788)), broad-winged hawk (*Buteo platypterus* (Vieillot, 1823)), barred owl (*Strix varia* (Barton, 1799)), great horned owl (*Bubo virginianus* (Gmelin, 1788)), red fox (*Vulpes vulpes* (L., 1758)), gray fox (*Urocyon cinereoargenteus* (Schreber, 1775)), coyote (*Canis latrans* (Say, 1823)), bobcat (*Lynx rufus* (Schreber, 1777)), raccoon (*Procyon lotor* (L., 1758)), mink (*Neovison vison* (Schreber, 1777)), least weasel (*Mustela nivalis* (L., 1766)), ermine (*Mustela erminea* (L., 1758)), long-tailed weasel (*Mustela frenata* (Lichtenstein, 1831)), fisher (*Martes pennanti* (Erxleben, 1777)), striped skunk (*Mephitis mephitis* (Schreber, 1776)), and opossum (*Didelphis virginiana* Kerr, 1792); Bumann 2002). A detailed site description is available in Tirpak et al. (2005).

During the spring (March-April) and fall (August-October) from 1998 to 2001, we used modified shorebird traps (Liscinsky and Bailey 1955) to capture grouse. We sexed each bird according to standard feather criteria (Roussel and Ouelett 1975) and fitted each with an aluminum leg band and 10 g necklace-style radio transmitter (Advanced Telemetry Systems, Isanti, Minnesota) prior to release. During the nesting period (March-July), 1999-2002, we used handheld receivers and two-element Yagi antennae to monitor hens for signs of incubation (i.e., found repeatedly at the same location). We flushed birds suspected of incubating to visually confirm nests and record the number of eggs. We conducted all subsequent monitoring remotely until the hen had ceased incubation (i.e., found repeatedly away from the nest site), when a second visual inspection of the nest was made to determine its fate and the number of eggs hatched. To determine brood habitat use and survival, we flushed successfully nesting hens (i.e., those hatching  $\geq 1$  egg) at 3 and 5 weeks post hatch and counted chicks. Brood flushes were conducted by two or more observers approaching the hen from opposite directions to maximize visual coverage of the brood. Counts deemed incomplete warranted a second flush; counts determined to be underestimates based on later counts were corrected to reflect the minimum number alive at that date. Using the number of hatched eggs as initial brood size, we calculated a daily survival rate through week 5 for each brood using the Flint et al. (1995) correction to the Mayfield (1961) estimator that allows for dependence among brood mates. Coordinates were recorded at all brood flush locations using global positioning system receivers, and these locations were coupled with the respective nest position and reliable (<10 ha error ellipse and <800 m from a known telemetry station; Tirpak 2005) triangulation estimates for brooding hens to provide a set of location estimates for the entire brood during the first 5 weeks post hatch. We defined utilization distributions for broods with five or more location estimates.

To assess brood habitat use at the site scale, we sampled vegetation at all brood flush sites. However, we only analyzed data from week 5 flushes to ensure a consistent time-frame across spatial scales and avoid pseudoreplication. To characterize available habitat, we located a paired random site by walking a random bearing and distance (50–100 m) from the brood site. We constrained the random site to this distance to ensure sampling included habitats simultaneously close enough to the encounter location to be considered im-

Habitat characteristics	Brood $(n = 21)$	Systematic $(n = 145)$
Basal area (m <sup>2</sup> /ha)	$13.2 \pm 2.3^{a}$	14.2±1.0
Percentage deciduous canopy cover of trees (≥8 cm DBH)	77.4±4.4	81.0±2.0
Percentage coniferous canopy cover of trees (≥8 cm DBH)	$0.0 \pm 0.0$	0.9±0.3
Ground cover (percentage of herbaceous or woody vegetation $\leq 1$ m tall)	71.9±4.5	57.4±2.3
Coarse woody debris cover (percentage of dead woody vegetation ≥15 cm in diameter)	12.4±2.9	12.4±1.0
Stems (<8 cm DBH and $\geq$ 1.5 m high) per hectare	22 352±2 127	15692±1060
Distance to road or opening class		
Close (<10 m)	$52.4^{b}$	39.3
Moderate (11–100 m)	38.1	51.7
Far (>100 m)	9.5	9.0
Midstory (>1 m high to bottom of canopy) volume class		
Open (<20%)	19.0	6.9
Moderate (20%–50%)	47.6	65.5
Closed (>50%)	33.3	27.6
Understory (≤1 m high) composition class		
Open (<20% woody and <30% herbaceous)	23.8	30.3
Herb (>30% herbaceous vegetation)	71.4	46.2
Wood (>20% woody vegetation)	4.8	23.4
Slope class		
Gentle (0%–10%)	76.2	65.5
Moderate (11%–30%)	23.8	24.1
Steep (>30%)	0.0	10.3

**Table 1.** Site-scale habitat characteristics at ruffed grouse (*Bonasa umbellus*) brood flush locations and random–systematic sites, 5 weeks post hatch, Moshannon State Forest, Pennsylvania, 1999–2002.

<sup>a</sup>Values are means ± SE for continuous variables.

<sup>b</sup>Percentage of total in each class for categorical variables.

mediately available to the brood and far enough to be independent of the habitat at the site being selected. To refine our characterization of available habitat, we also sampled habitat along a systematic array of points located at ~500 m intervals throughout the study area.

At all sites, we measured habitat in 0.04 ha circular plots (Noon 1981). We recorded the percent cover for deciduous and coniferous canopy, ground vegetation, and coarse woody debris by recording the presence or absence of each of these variables at 10 equally spaced ocular tube sightings along the north-south and east-west axes of the plot (20 points total). We estimated stem density (stems/ha) by counting all woody stems (<8 cm diameter at breast height (DBH) and >1.5 m tall) in 2 m wide strips along these same axes. Basal area (m<sup>2</sup>/ha) was estimated using a 10-factor prism (ft<sup>2</sup>/ac converted to m<sup>2</sup>/ha). Additionally, we classified slope, distance to the nearest road or opening, timber size class, midstory vegetation volume, and understory type for each plot (Table 1). Vegetation sampling at brood and random sites was completed within 1 week of the encounter date. Sampling at systematic sites was conducted during the brood periods (June-August), 2001 and 2002.

To assess brood habitat use at the landscape scale, we used the Animal Movement Extension to ArcView version 3.3 (Hooge and Eichenlaub 2000) to construct 95% fixed-kernel utilization distributions from the full complement of location estimates for individual ruffed grouse broods. Least-squares cross-validation was used to estimate the smoothing factor for all kernels (Seaman and Powell 1996). To characterize available habitat at the landscape scale, we generated 200 random points per site and buffered each with a circle equivalent to the average circular utilization

distributions area for all broods (78.8 ha). This approach represents the distribution of potential habitat compositions available to individuals more accurately than simply utilizing the proportion of each habitat type in the overall landscape (Katnik and Wielgus 2005). To determine the habitat composition of the empirical and simulated brood utilization distributions, we used the XTools extension to ArcView version 3.3 (DeLaune 2003) to intersect the kernels with data layers depicting 15 habitat types from 5 main habitat classes: topographic moisture index, overstory type, forest stand age, understory type, and road (Table 2). These layers were derived from a combination of classified Landsat Thematic Mapper imagery, digital elevation models, and pre-existing data sets (see Tirpak (2005) for detailed descriptions of these data sets). The area of each habitat type was calculated and converted to a percentage of each kernel or buffer.

To assess brood habitat selection at the site scale, we employed case-control conditional logistic regression (Ramsey et al. 1994; Compton et al. 2002), with each matched set consisting of a brood location (case) and all other sample points (controls) located within 501 m of it. We used this distance to reflect the radius of the average circular utilization distribution for broods in this study (78.8 ha). We assumed all habitats within this distance were available to ruffed grouse broods at any point in the brood period. Similarly, we used logistic regression to assess brood habitat selection at the landscape scale by comparing the habitat composition between brood and randomly-generated utilization distributions. Because habitat features were not mutually exclusive, we relaxed unit-sum constraints (e.g., a habitat type is selected because another is avoided) by elim-

Habitat characteristics	Brood $(n = 28)^a$	Systematic $(n = 200)^a$
Topographic moisture index		
Mesic	10.2±1.3	10.4±0.5
Mesoxeric	18.2±1.2	23.6±0.8
Xeric	71.5±2.3	66.0±1.1
Overstory type		
Agriculture	$0.0 \pm 0.0$	0.1±0.0
Bare ground	0.6±0.2	0.3±0.1
Evergreen	2.9±0.7	7.5±0.8
Non-oak deciduous	75.4±3.6	59.7±2.0
Oak deciduous	21.0±3.7	32.2±2.2
Water	0.1±0.1	0.3±0.1
Forest stand age		
1- to 10-year-old forest	$0.0 \pm 0.0$	0.0±0.0
10- to 20-year-old forest	36.1±3.9	10.5±1.5
>20-year-old forest	63.3±4.0	88.8±1.5
Understory type		
Nonevergreen	86.5±2.3	81.2±1.4
Evergreen	9.8±2.3	10.6±0.9
Road		
Road	4.3±0.5	3.0±0.2

**Table 2.** Comparison of landscape-scale habitat characteristics within utilization distributions of ruffed grouse (*Bonasa umbellus*) broods through 5 weeks post hatch between flush and random locations, Moshannon State Forest, Pennsylvania, 1999–2002.

<sup>*a*</sup>Percentage values are means  $\pm$  SE.

inating one variable from any highly correlated pairs ( $r \ge 0.70$ ). General linear models were employed to determine habitat characteristics associated with higher daily survival rates at both the site and landscape scales.

Based on our field experiences and a review of the literature, we developed a set of 25 candidate models to differentiate used (brood) and available (random and systematic) habitat and characterize the relationship between habitat conditions and brood survival at the site and landscape scales (Compton et al. 2002). We tested these candidate models using Akaike's information criterion adjusted for small sample size, AIC<sub>c</sub>. Models with  $\Delta AIC_c \leq 2$  were considered supported. We used Akaike weights (*w*) to rank variable importance and adjust coefficients and odds ratios of competing models (Burnham and Anderson 1998).

## Results

During the 4 years of this study we located 69 nests, 38 of which were successful and produced broods (brood size at hatch =  $8.3 \pm 0.4$  chicks (mean  $\pm$  SE), range = 3-13 chicks). We flushed all broods at weeks 3 and 5 and measured site-level habitat characteristics at flush locations for 21 of these broods. We recorded complete counts for 19 of these broods, for which we estimated an average daily survival rate of 0.966  $\pm$  0.005 (range = 0.920–0.997) through week 5. We had sufficient locations to calculate utilization distributions for 28 broods.

Our data supported one model of brood habitat selection at the site scale (w = 0.883), which contained three variables: percentage ground cover, understory composition class, and small stem density. Broods were ~70% more likely to occupy a site with each 10% increase in percentage ground cover and exhibited a strong preference for herbaceous and open understories over those dominated by woody vegetation (Table 3). Additionally, higher small stem densities were associated with higher brood use, with a  $\sim 12\%$  increase in the likelihood of a brood using a site for every increase of 1000 stems/ha.

Two models relating site-level habitat characteristics to daily survival rate had  $\Delta AIC_c \leq 2$ . The top model ( $\Delta AIC_c = 0.000$  and w = 0.349) contained the categorical variable distance to road or opening, as well as percentage of dead woody cover. The other supported model ( $\Delta AIC_c = 1.952$  and w = 0.132) contained these two variables, as well as percentage of ground cover. Relative to the base daily survival rate observed at moderate distances (0.946), broods far from roads or openings had a 0.020 lower daily survival, while those close to roads had a rate 0.016 higher. Increasing percentages of coarse woody debris or ground cover also improved survival rates, albeit with a less pronounced effect (0.008 and 0.001 for a 10% increase in each variable, respectively).

Three models of brood habitat selection at the landscape scale were supported (Table 4). We evaluated the importance of individual model variables separately because of the relatively equal Akaike weight associated with each model (Burnham and Anderson 1998). Forest in the 10- to 20-year age class (w = 0.575) occurred in all models and was positively related to the occurrence of broods at the landscape scale (Table 5). Mesic and mesoxeric forest (w = 0.467) occurred in the top two models, with a negative association between broods and increasing proportions of mesoxeric habitat. Road density had the third highest weight (w = 0.315), but was the strongest predictor of brood habitat at the landscape scale. Evergreen understory and non-oak hardwood overstory were also positively associated with broods; habitats with evergreen overstories were avoided by broods.

Table 3. Akaike-weighted odds ratios of variables occurring in Akaike's information criterion corrected for small sample sizes (AIC<sub>c</sub>) supported models of ruffed grouse (Bonasa um*bellus*) brood (n = 21) habitat selection at the site scale, 5 weeks post hatch, Moshannon State Forest, Pennsylvania, 1999-2002.

				90% CI	
Variable	$\beta$	SE	Odds ratio	Lower	Upper
UNDER_OPEN <sup>a</sup>	5.705	2.083	300.441	9.763	9245.461
UNDER_HERB <sup>a</sup>	5.251	1.854	190.677	9.035	4024.022
$\operatorname{GROUND}^{b}$	0.523	0.223	1.697	1.176	2.448
STEM <sup>c</sup>	0.110	0.033	1.117	1.057	1.180

Note:  $\beta$ , slope; CI, confidence interval.

"Understory ( $\leq 1$  m high) volume class (%): OPEN (< 20% woody and < 30% herbaceous) and HERB (>30% herbaceous vegetation).

<sup>b</sup>Ground cover (% herbaceous or woody vegetation  $\leq 1$  m tall). Estimated for 10% change.

Woody stems (<8 cm DBH and  $\geq$ 1.5 m high) per hectare. Estimated for 1000 stem/ha change.

Table 4. Summary of a priori models of ruffed grouse (Bonasa umbellus) brood habitat selection at the landscape scale through 5 weeks post hatch and its influence on brood survival, Moshannon State Forest, Pennsylvania, 1999–2002.

Model <sup>a</sup>	k	AICc	$\Delta \operatorname{AIC}_{c}$	w
Landscape habitat selection				
$MESIC^{b} + MESOXERIC^{c} + 20^{d}$	3	143.135	0.000	0.258
MESIC + MESOXERIC + ROAD $^{e}$ +20	4	143.569	0.434	0.208
ROAD + 20 + EVER_UNDER <sup>f</sup> + EVERGREEN <sup>g</sup> + HARDWOOD <sup>h</sup>	5	144.858	1.723	0.109
Landscape effects on survival				
ROAD	2	-147.489	0.000	0.282
ROAD + 20	3	-147.240	0.249	0.249

**Note:** k is the number of model parameters; w is the Akaike weight.

<sup>a</sup>Only models supported by Akaike's information criterion corrected for small sample sizes are presented ( $\Delta AIC_c < 2$ ).

<sup>b</sup>Moist sites, typically low elevation, east or north aspect, low slope, or concave landform.

"Sites exhibiting both mesic and xeric characteristics (e.g., concave landform on west aspect).

<sup>d</sup>Forest stands initiated between 1980 and 2002.

<sup>e</sup>Access routes utilized for transportation, includes unpaved roads, logging roads, and trails.

<sup>f</sup>Deciduous forest stands with >10% evergreen shrubs and >20% of all shrub cover is evergreen.

<sup>g</sup>Forest stands dominated by trees that remain green year-round.

<sup>h</sup>Forest stands dominated by deciduous trees, excluding oak.

Road density and 20-year-old forest were the only two variables included in the models relating landscape-scale habitat to brood survival (Table 4). Road density negatively affected brood survival with a 0.004 reduction in daily survival rate with each 1% increase in road density within the utilization distribution. Conversely, broods benefited from increased proportions of 20-year-old forest within the utilization distribution (Table 5).

### Discussion

Broods in this study selected roads and young deciduous forest habitats containing a dense understory of herbaceous vegetation and a high density of small stems. The use of early successional stands with high small stem densities by broods has been noted by many researchers (Bump et al. 1947; Sharp 1963; Kubisiak 1978; Landry 1982; Scott et al. 1998; Giroux et al. 2007). However, the majority of these studies were conducted in aspen-dominated forests where the connection between grouse and aspen is well-documented (Rusch and Keith 1971; Svoboda and Gullion 1972). Alternatively, mid-age and mature forest stands are commonly utilized by broods in non-aspen forests (Freiling 1985; Fettinger 2002; Haulton et al. 2003). Although aspen was present on our site, it was restricted to a small (~350 ha) tornado-impacted stand that had subsequently burned. Nevertheless, we flushed most broods (14 of 21) in or adjacent to sapling stands, although relatively few broods (5 of 21) actually were detected in the aspen stand itself.

Our observation of broods in young forest stands not dominated by aspen likely reflects the preference of broods for habitats with both abundant ground cover and high small stem densities, as well as the availability of those habitats on our site. Although mature forest stands generally had higher amounts of ground cover than younger stands on our site  $(63.0\% \pm 3.3\%$  (mean  $\pm$  SE) vs.  $54.3\% \pm 3.0\%$ , respectively), the locations where we flushed broods within sapling habitats typically had high ground cover percentages as well  $(65.7\% \pm 5.3\%)$ . This level of ground cover was consistent with those reported by Thompson et al. (1987; 64.8%) and Haulton et al. (2003; 62.6%) for brood habitat in more mature oak forests. However, small stem densities in sapling stands on our site were approximately twice those observed in mature forest habitats  $(19423 \pm 1219 \text{ vs. } 9019 \text{ vs. } 9019 \text{ vs. } 9019 \text{ vs. }$ 

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**Table 5.** Akaike-weighted regression coefficients and odds ratios for variables occurring in Akaike's information criterion corrected for small sample sizes (AIC<sub>c</sub>) supported models of ruffed grouse (*Bonasa umbellus*) brood habitat selection at the landscape scale and the influence of landscape-scale habitat on brood survival through 5 weeks post hatch, Moshannon State Forest, Pennsylvania, 1999–2002.

				90% CI <sup>a</sup>	
Variable	$\beta$	SE	Odds ratio	Lower	Upper
Landscape selection					
$MESIC^{b}$	0.348	0.360	1.416	0.783	2.561
MESOXERIC <sup>c</sup>	-0.739	0.312	0.478	0.286	0.797
$20^{d}$	0.378	0.087	1.459	1.264	1.683
ROAD <sup>e</sup>	1.256	0.858	3.513	0.856	14.417
EVER_UNDER <sup>f</sup>	0.407	0.200	1.502	1.081	2.088
EVERGREEN <sup>g</sup>	-0.776	0.509	0.460	0.199	1.063
$HARDWOOD^h$	0.209	0.122	1.233	1.009	1.506
Landscape influence on survival					
CONSTANT	0.977	0.010		0.961	0.993
$20^{i}$	0.003	0.002	_	-0.001	0.006
ROAD	-0.004	0.002	—	-0.007	-0.001

**Note:**  $\beta$ , slope; CI, confidence interval.

<sup>a</sup>90% CI applies to odds ratio values for variables associated with landscape selection and to regression coefficients for variables associated with landscape influence on survival.

<sup>b</sup>Moist sites, typically low elevation, east or north aspect, low slope, or concave landform.

<sup>c</sup>Sites exhibiting both mesic and xeric characteristics (e.g., concave landform on west aspect).

<sup>d</sup>Forest stands initiated between 1980 and 2002.

<sup>e</sup>Access routes utilized for transportation, includes unpaved roads, logging roads, and trails.

<sup>f</sup>Deciduous forest stands with >10% evergreen shrubs and >20% of all shrub cover is evergreen.

<sup>g</sup>Forest stands dominated by trees that remain green year-round.

<sup>h</sup>Forest stands dominated by deciduous trees, excluding oak.

<sup>i</sup>Estimated for a 10% change.

1640 stems/ha, respectively). Given similar ground cover values, the additional security provided by the higher small stem densities in the 10- to 20-year-old forest likely made these sites more attractive to broods. Studies where high small stem densities were not selected were typically in non-aspen habitats as well (Freiling 1985; Thompson et al. 1987; Dobony 2000; Fettinger 2002; Haulton et al. 2003). Although these authors found broods in habitats with lower small stem density than generally available, this may be due to limited ground cover in habitats with high small stem densities rather than a lack of preference for high small stem densities per se. Light attenuation is lower through aspen canopies than other hardwood forest types; therefore, more light reaches the understory in aspen forests and a denser understory can develop, even under similar amounts of canopy closure (Canham et al. 1994; Constabel and Lieffers 1996). Early successional stands with stem densities comparable to those used by broods in aspen-dominated forest may not contain enough ground cover to attract grouse broods occurring outside the range of aspen. Our site may have been an exception because of the heterogeneous canopy conditions produced by the tornado, which permitted higher levels of light to reach the forest floor in some locations and permitted the development of ground cover conditions favorable to grouse broods.

Ground cover vegetation is directly related to the abundance of arthropod prey that makes up the bulk of the grouse diet in the first few weeks post hatch (Kimmel and Samuel 1978; Dobony 2000). Therefore, suitable ground cover is likely the primary factor driving brood habitat selection. Indeed, the amount and composition of ground cover were stronger predictors of brood habitat than stem density. In fact, only Giroux et al. (2007) observed selection for habitats with high stem density without a concurrent selection for high ground cover. Conversely, a number of authors have documented the inverse (Stauffer and Peterson 1985; Thompson et al. 1987; Haulton et al. 2003).

Higher ground cover and coarse woody debris in young forest stands also improved daily survival rate. The prevalence of habitats with this combination on our site may explain why it had greater brood survival than most other sites in the central and southern Appalachians (Tirpak et al. 2006). Ground cover is generally hypothesized to provide some concealment from predators (Stewart 1956; Godfrey 1975; Thompson et al. 1987; Tirpak et al. 2005), while coarse woody debris is likely an important component of escape cover (Kubisiak 1978; Rogers and Samuel 1984). Although these factors are hypothesized to reach maxima above which broods are negatively affected (Gullion 1970; Kubisiak 1978; Healy 1985), we did not observe thresholds in these values. No brood occurred on sites with <35% ground cover, and 9 of 24 broods occurred in habitats with  $\geq 80\%$  ground cover — the highest value observed on sites used by broods in Michigan (Berner and Gysel 1969). Furthermore, we observed broods utilizing habitats with high amounts of dead woody cover (45%) and commonly observed chicks retreat beneath large logs and slash piles during flush counts.

Roads, mostly old logging roads and gated forest roads through tornado-impacted areas that had been salvaged, were strongly selected by broods in this study. These roads typically contained a well-developed herbaceous layer and were either completely canopied or immediately adjacent to forest stands. Use of these habitats is well-documented, particularly in the central and southern Appalachians (Stewart 1956; Hollifield and Dimmick 1995; Whitaker et al. 2006). Their high use in this region may reflect the limited areas where adequate herbaceous ground cover occurs in conjunction with preferred small stem densities (Hollifield and Dimmick 1995). Herbaceous cover and sapling density are typically highest in edge habitats (Fraver 1994; Gehlhausen et al. 2000), and roads and trails are likely the dominant edge habitats in many central and southern Appalachian forests (Kochendorfer 1977; Semlitsch et al. 2007). Broods are commonly associated with edge habitats throughout their range, although not specifically with roads as in the Appalachians (Bump et al. 1947; Porath and Vohs 1972; Maxson 1978; Scott et al. 1998; Fearer and Stauffer 2003; Giroux et al. 2007).

Although we observed increased survival with increasing proximity to an edge at the site scale, we observed a negative relationship between road density and brood survival rate at the landscape scale. This apparent contradiction likely reflects the differential scale at which the arthropod prey and the potential predators of grouse broods exhibit a numerical response. Arthropod abundance is inversely related to distance from edge (Jokimäki et al. 1998). Therefore, birds occupying interior habitats may have less access to potential prey items than birds along edges. This greater availability of food along edges may decrease foraging times and travel distances, which, in turn, reduces the overall exposure of the brood to predators and increases their survival. Conversely, grouse predators perceive fragmentation at broader scales due to their large body and home range size (Chalfoun et al. 2002; Gehring and Swihart 2003). For example, bobcats exhibit a preference for high contrast edges but only at the scale of the home range (Constible et al. 2006). Similarly, opossums are more abundant in highly fragmented landscapes but show no preference for edge habitats (Dijak and Thompson 2000). Grouse occupying landscapes highly fragmented by roads may benefit from an increased availability of arthropod prey, but suffer higher predation rates in these habitats. In this study, road densities above 4%-5% were associated with the lowest daily survival rates. This proportion of road may represent a threshold value above which the benefit of increased arthropod availability is offset by higher predator abundance.

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