



Research Article

Evaluating Spatially Explicit Viability of a Declining Ruffed Grouse Population

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ABSTRACT Species associated with early successional habitats have experienced dramatic declines in the eastern United States as a result of land use changes and human disruption of natural disturbance regimes. Consequently, active management is required to create early successional habitat and promote plant and animal communities that depend on periodic forest disturbance. Ruffed grouse (*Bonasa umbellus*) depend on recently disturbed forest habitat, and have experienced dramatic declines over the last half-century. Although ruffed grouse are extensively studied, little effort has been made to link population dynamics with habitat management at landscape scales. We used stochastic, spatially explicit population models that combined landscape conditions derived from a Geographic Information System with demographic data, and applied the model to a declining ruffed grouse population in Rhode Island, USA. We identified vital rates that influence ruffed grouse population dynamics using baseline models constructed with current demographic rates and landscape conditions, and assessed the effect of landscape-scale forest management alternatives on population persistence by running multiple management simulations. Baseline models typically predicted population decline, and we concluded that vital rates (survival and recruitment) had a greater influence on population persistence than did dispersal capability, carrying capacity, or initial population size. Management simulations predicted greater population persistence under a scenario where high-quality habitat was provided in fewer large blocks as opposed to many small blocks, and the rate at which we allowed ruffed grouse to colonize newly created habitat had a substantial impact on management success. Populations of ruffed grouse in the eastern United States are likely to continue to decline given current disturbance regimes, and our work provides a link between ruffed grouse demography and landscape-scale habitat conditions to support management decisions. © 2011 The Wildlife Society.

KEY WORDS *Bonasa umbellus*, early successional forest, forest disturbance, forest management, population viability, PVA, Rhode Island, ruffed grouse.

Ruffed grouse (*Bonasa umbellus*) populations have declined in excess of 50% over the last half-century (Rusch et al. 2000, Dessecker and McAuley 2001, Butcher and Niven 2007). Ruffed grouse are most commonly associated with recently disturbed forest habitat in the primary stages of tree and shrub regeneration (Dessecker and McAuley 2001). These early successional forests provide the vegetation structure and composition required by ruffed grouse for breeding (Stoll et al. 1979), brood rearing (Thompson et al. 1987, Scott et al. 1998), juvenile dispersal (Small and Rusch 1989), and adult habitat use (Whitaker et al. 2006). Early successional forest is

generally considered a limiting component of ruffed grouse habitat (Dessecker and McAuley 2001), and reduced availability of early successional forest is commonly invoked as the primary contributor to ruffed grouse population declines (Rusch et al. 2000, Dessecker and McAuley 2001, Norman et al. 2004).

Recent declines in early successional vegetation types, and associated wildlife, have received considerable attention in the eastern United States (Askins 2000, Dessecker and McAuley 2001, Litvaitis 2001, Dettmers 2003, Fuller and DeStefano 2003). Changing land use has modified natural disturbance regimes and reduced availability of early successional forests in the region. Now these habitats may cover less area than prior to European settlement (Brooks 2003, Litvaitis 2003, Lorimer and White 2003). This has spurred considerable conservation attention, but management prescriptions such as timber harvest and prescribed fire that create and maintain early successional habitat are often

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controversial, especially on multiple-use public lands (Askins 2001, Litvaitis 2003). Thus, empirical support is needed to better-inform management decisions that promote early successional species such as ruffed grouse.

Even when evidence for population decline is clear, and species' habitat relationships are thought to be well understood, population response to management may be uncertain because empirical studies often focus on habitat use and selection without establishing a causal link to more biologically relevant response variables (e.g., individual fitness or population viability; Wolff 2000). If a direct linkage between population dynamics and resource use and availability can be drawn, the mechanisms responsible for population regulation can be identified more clearly (Aldridge and Boyce 2007). Spatially explicit population models that combine habitat affiliations with specific demographic data provide such a link, may be especially useful to predict population response to habitat change (Beissinger and McCullough 2002, Reed et al. 2002, Beissinger et al. 2006), reduce uncertainty, and justify management decisions.

Ruffed grouse habitat relationships have been frequently studied at relatively fine spatial extents (i.e., individual management blocks or study areas; Bump et al. 1947, Robinson 1984, Gullion 1984c, Rusch et al. 2000, Norman et al. 2004), but these focused studies are limited in their ability to answer population-level questions across broader geographic areas (e.g., states or ecoregions). Recently, a major research initiative (Norman et al. 2004) has greatly improved our knowledge of ruffed grouse demography across the southern portion of the species' range (Tirpak et al. 2006, Devers et al. 2007). However, little has been done to link these demographic data to habitat availability at similarly broad extents, and many questions related to landscape-level management remain unresolved (Rusch et al. 2000). For example, given that active forest management for ruffed grouse is controversial and can fragment intact mature forests, should managers focus on creating fewer large areas of ruffed grouse habitat even though this may sacrifice demographic connectivity? What demographic rates are likely to limit ruffed grouse populations that use these disconnected habitats? Ideally, such questions would be answered using well-designed field experiments, but modeling may offer an efficient preliminary step toward testing predictions across broad spatial extents.

As a first step toward linking ruffed grouse population demography with habitat distribution and management at the landscape scale, we developed a spatially explicit population model for a declining ruffed grouse population in a landscape of management concern in Rhode Island, USA (Fig. 1). Rhode Island is a convenient model system for ruffed grouse because habitat conditions, land use history, and ruffed grouse habitat affiliations are generally similar to those across the southern extent of the species' range where declines are most pronounced, and for which extensive demographic data are available (Rusch et al. 2000, Norman et al. 2004). Our specific objectives were to 1) develop a spatially explicit model of ruffed grouse population viability, 2) identify which population parameters (stage-specific sur-

vival and reproduction rates, dispersal, carrying capacity, abundance) have the greatest influence on model outcome, 3) assess the relative effects of different landscape-scale habitat management strategies on population viability, and 4) provide management recommendations based on model results.

STUDY AREA

Our study area was a 735-km² landscape in southwestern Rhode Island (41° 24' to 42° 43' N, and from 71° 47' to 71° 32' W; Fig. 1). We selected this landscape because it encompassed approximately 92% of state-controlled wildlife management areas in the southern half of the state. Additionally, this area included the site of all previous ruffed grouse research in the state (Devers 2005, Endrulat et al. 2005, Blomberg et al. 2009). The majority of the study area was forested (>61%). Forest stands dominated by deciduous species such as oak (*Quercus* spp.), hickory (*Carya* spp.), and American beech (*Fagus grandifolia*) were common, and comprised >58% of the total forest cover in the study area. Coniferous stands dominated by pine (*Pinus* spp.), and mixed hardwood/conifer stands, comprised 10% and 29% of the forests in the study area, respectively. Although early successional forest habitat was once common, during our study <1% of the study area contained early successional forest of sufficient area to support ruffed grouse (Blomberg et al. 2009). Consequently, ruffed grouse relied heavily on alternative low-quality habitats in the study area such as riparian corridors and mixed deciduous/coniferous stands (Endrulat et al. 2005, Blomberg et al. 2009).

METHODS

Population Model

We developed spatially explicit, stage-based stochastic simulation models for ruffed grouse population viability (RAMAS GIS Version 5, Applied Biomathematics, Setauket, NY; Akçakaya 2005). Our initial population model was comprised of 3 main components: 1) a spatial model that identified distribution of habitat patches across the study area and defined the population spatial structure, 2) a vital rate matrix model that predicted population growth in each patch through time while accounting for density dependent and stochastic processes, and 3) a dispersal model that defined the proportion of individuals exchanged between patches.

Population spatial structure.—We used a spatial model of ruffed grouse habitat distribution (Blomberg et al. 2009; Fig. 1) to define the population's spatial structure. Blomberg et al. (2009) used a partitioned Mahalanobis D^2 procedure (Rotenberry et al. 2006) to predict a continuous surface of habitat probability across the study area based on similarities to known grouse locations and relative distance to multiple landscape features. A probability threshold value was used to delineate habitat from non-habitat, and 82 discrete patches of ruffed grouse habitat were identified that cover 10,582 ha (approx. 14% of the study area). Additional information on habitat conditions and criteria used to delineate patches is described in detail in Blomberg

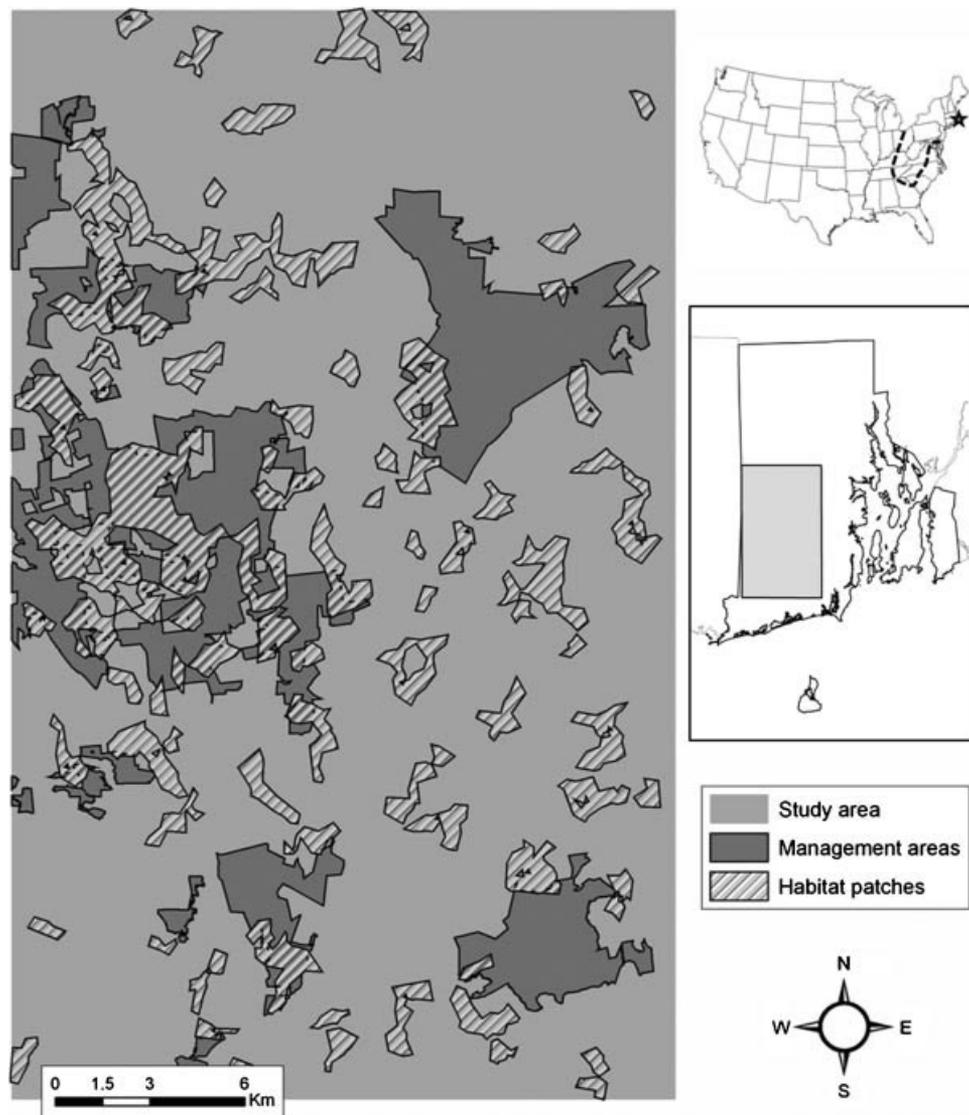


Figure 1. Locations of ruffed grouse habitat patches used to define a spatial structure for a spatially explicit, stochastic model of ruffed grouse population viability in southwestern Rhode Island, USA. State-owned management areas where simulated habitat units were added are identified in dark gray. The extent of the area depicted by the left figure pane is shown within the map of Rhode Island to the right. The approximate southeastern limit of ruffed grouse distribution is indicated by the dashed line on the inset map of the United States.

et al. (2009). Because this model is not explicitly tied to any measure of grouse success (i.e., survival or reproduction), for the purpose of this study we assumed no heterogeneity in quality among existing patches. We assumed all patches to be occupied at the beginning of each simulation. The study area did not represent a discrete single population, so we assumed that ruffed grouse movement into or out of the study area was unrestricted and that immigration and emigration were equivalent.

Although current ruffed grouse densities in Rhode Island were generally low (Tefft 2007), no quantified density estimates were available. Gullion (1984c) suggested that when ruffed grouse habitat contains a substantial conifer component, grouse are found in densities of 2–3 birds per 100 ha. In our spatial model, areas that contained mixed conifer forests were regularly predicted as grouse habitat (Blomberg et al. 2009), and grouse are known to select such habitats (Endrulat et al. 2005). We assumed the level of conifer

presence in grouse habitat in southern Rhode Island reflected conditions relevant to Gullion's (1984c) density estimate, and defined the initial abundance for each habitat patch as the patch area divided by 50 ha, rounded to the nearest whole grouse. This resulted in initial abundance of 191 ruffed grouse in the study area.

Vital rates.—Ruffed grouse are polygamous with all parental care provided by females (Rusch et al. 2000), so we modeled only females. We used a 2-stage life cycle for ruffed grouse consisting of subadult (<1 yr old) and adult (≥ 1 yr old) age classes, and assumed a stable age distribution. Because limited demographic data prevented us from estimating a single set of vital rates for Rhode Island, we developed baseline models using survival and recruitment estimates from the recently completed Appalachian Cooperative Grouse Research Project (ACGRP; Norman et al. 2004; Table 1). These included all available demographic data specific to Rhode Island, as well as data for

Table 1. Means and standard deviations (SD) of parameter values that were used to assess the influence of each parameter on a spatially explicit, stochastic simulation of ruffed grouse population viability in southwestern Rhode Island, USA.

Parameter	Min.	SD	Median	SD	Max.	SD
Subadult recruitment	0.087 ^{a,b}	0.073	0.353 ^{a,b}	0.128	0.476 ^a	0.231
Adult recruitment	0.112 ^{a,b}	0.085	0.386 ^{a,b}	0.148	0.627 ^a	0.348
Subadult survival	0.3 ^c	0.127	0.49 ^d	0.1	0.522 ^a	0.148
Adult survival	0.3 ^c	0.127	0.49 ^d	0.1	0.569 ^a	0.167
Dispersal rate	0.7 ^e	NA	0.8 ^e	NA	0.9 ^f	NA
Average dispersal distance (m)	1,402 ^e	732	2,673 ^e	1,314	4,820 ^g	3,255
Initial abundance (F/ha)	1/100 ^h	NA	1/50 ^h	NA	1/25 ^h	NA
Carrying capacity (F/ha)	1/50 ^h	NA	1/25 ^h	NA	1/12.5 ^h	NA

^a Tirpak et al. (2006).

^b Parameter value modified from Tirpak et al. (2006) to reflect additional mid-summer chick mortality.

^c Devers (2005).

^d Devers et al. (2007).

^e Smith (2006).

^f Yoder (2004).

^g Small and Rusch (1989).

^h Values estimated during this study.

ruffed grouse inhabiting oak-dominated forests in Virginia (36° 17' N, 89° 41' W) and West Virginia (37° 51' N, 80° 19' W). We selected the Virginia and West Virginia sites as sources of supplemental vital rate information because they have similar forest compositions (Haulton 1999, Haulton et al. 2003), and relative phenology indices (Devers et al. 2007), when compared to ruffed grouse habitat in southern Rhode Island. We used survival estimates for Rhode Island grouse reported by Devers (2005) and for West Virginia reported by Tirpak et al. (2006). For recruitment, we selected estimates from sites in Virginia and West Virginia reported by Tirpak et al. (2006; Table 1).

Vital rate values were derived from hunted populations with varying degrees of harvest pressure. Based on results of manipulative harvest experiments in the region (Devers et al. 2007), we assumed that harvest mortality was compensatory, and variation in survival between populations did not result from differing harvest rates.

For their fecundity estimates, Tirpak et al. (2006) included survival of chicks to 35 days post-hatch, and assumed no chick mortality between age 35 days and their census on 1 September (J. Tirpak, United States Fish and Wildlife Service, personal communication). Although summer chick survival is apparently very high (Larson et al. 2001), ruffed grouse suffer some summer mortality (Devers et al. 2007). Consequently, we assumed that chicks >35 days old were subject to late-summer mortality similar to that of adult birds. At 35 days of age, ruffed grouse chicks are able to self-thermoregulate (Bump et al. 1947, Rusch et al. 2000), and although they remain socially aggregated, they are largely independent of the hen (Gullion 1984a). We used July and August survival estimates for adult ruffed grouse (0.96 and 0.98, respectively; Devers et al. 2007), and modified the fecundity model from Tirpak et al. (2006) to calculate recruitment, R , of chicks into the subadult breeding population as

$$R = S_J \times S_A \times (F)$$

where S_J = July survival, S_A = August survival, and F = fecundity as estimated by Tirpak et al. (2006). We incorporated the corrected recruitment values into Leslie projection matrices

$$V = \begin{bmatrix} R_s & R_a \\ S_s & S_a \end{bmatrix}$$

where the upper matrix elements represent stage-specific recruitment rates, the lower elements represent stage-specific survivals, the left elements define subadults, and the right elements define adults. We structured the vital rate matrix assuming a post-breeding census.

Density dependence.—Data on density dependence in ruffed grouse vital rates are sparse. In their northern range, ruffed grouse populations are cyclical as part of the boreal forest's 10-year cycle, whereas more southerly populations of ruffed grouse, such as those found in Rhode Island, are non-cyclic (Rusch et al. 2000). Bergerud and Gratson (1988) suggested that density dependent nesting success could limit non-cyclic grouse populations, but Rusch et al. (2000) speculated that ruffed grouse populations were unlikely to be limited by density-dependant factors. Our preliminary simulations showed that when density independence was assumed, and vital rates were increased to simulate management, populations sometimes grew exponentially to unreasonably large sizes (e.g., millions of individuals). Thus, we imposed ceiling-type density dependence and set baseline carrying capacity (K) to $2 \times$ initial abundance ($K = 1$ female/25 ha).

Environmental stochasticity.—We used standard deviations reported by Tirpak et al. (2006) and Devers (2005; summarized in Table 1) as estimates of variance in vital rates

$$SD = \begin{bmatrix} \text{Var}(R_s) & \text{Var}(R_a) \\ \text{Var}(S_s) & \text{Var}(S_a) \end{bmatrix}$$

where the matrix elements share the position of their corresponding vital rates defined above. For each year, vital rates were sampled from a normal distribution defined by the mean and variance of each parameter, and all stochastic

simulations were run for 50 years and 1,000 replications. Stochastic factors that influence ruffed grouse vital rates (e.g., weather, mast production) are likely to influence both survival and fecundity. For example, in winters with greater snowfall, grouse are able to use snow for cover during roosting more regularly, which improves predator avoidance and leads to increased over-winter survival (Doerr et al. 1974, Rusch et al. 2000, Whitaker and Stauffer 2003) while also decreasing energetic costs of thermoregulation (Thompson and Fritzell 1988). Decreased metabolic requirements during winter would allow females to enter the breeding season with greater stored fat reserves, which are directly related to reproductive output (Long et al. 2004). We therefore assumed that survival and fecundity covary annually and that these vital rates were correlated among adjacent patches. The study area did not cover a large enough spatial extent that correlation should vary with distance, so we assumed strong vital rate correlation ($r = 0.70$) among all patches.

Dispersal.—We used values reported as part of the ACRP by Smith (2006) to estimate dispersal rates between patches. Because ruffed grouse complete natal dispersal prior to first breeding (<1 yr after hatch), and occupy relatively stable territories thereafter (Small et al. 1993, Rusch et al. 2000, Smith 2006), we only allowed subadults to disperse. Fall dispersal distances for ruffed grouse across all ACRP study sites were normally distributed (B. Smith, Kentucky Department of Fish and Wildlife Resources, personal communication), and average distance for females was 2,673 m (SE = 438 m; Smith 2006). The longest dispersal distance observed for a female ruffed grouse was 9,534 m (Smith 2006). Previous radio-telemetry studies within our study site suggest dispersing grouse move freely through forested areas and readily cross potential barriers (e.g., water bodies, major roads) during dispersal (E. J. Blomberg, University of Rhode Island, personal observation), so we assumed dispersal between patches was restricted only by distance. For patches within the maximum dispersal distance of one another, we calculated the proportion of individuals that dispersed between patches (modified from Kitching 1971, Akçakaya 2005) as:

$$M_{ij} = \frac{e^{((-D_{ij})/b)}}{\sum_i e^{((-D_{ij})/b)}}$$

where M is the proportion of subadults from patch i that disperse to patch j , D is the distance from the center of patch i to the edge of patch j , b is the average dispersal distance of female grouse, and the dispersal rate is a proportion of the sum of possible dispersers from patch i . In cases where patches were separated by a distance greater than the maximum dispersal distance, we set dispersal to 0.

Not all subadult grouse leave their natal territory, so we multiplied dispersal probabilities by 0.84, which is the dispersal rate for female grouse (Smith 2006). Some patches were large enough that an individual could disperse and still remain in the natal habitat patch. To account for within-patch dispersal, we created a buffer around the center point of

each patch with a radius equivalent to the average female grouse dispersal distance (2,673 m; Smith 2006). For patches with areas exceeding average dispersal distance, we defined within-patch dispersal as the proportion of the patch that fell outside this buffer. Total dispersal from such a patch was then discounted by this value, assuming an even distribution of individuals within the patch. This allowed us to better represent the proportion of individuals that dispersed from their natal territories, but in doing so did not leave the natal patch.

Parameter uncertainty.—To address uncertainty in our input parameters, we conducted single parameter perturbations to gauge the individual influence of survival, recruitment, dispersal rate, average dispersal distance, initial abundance, and carrying capacity on model results. Whenever possible we used maximum, minimum, and median values for each parameter as reported in the literature (Table 1). We first ran a model that used the median value for all parameters. We then ran perturbations where a single parameter was increased or decreased while all other parameters were held at median levels, and we interpreted the difference in model outcome from each perturbation as the relative importance of that parameter. Estimates of recruitment from oak-hickory forests were generally low (Tirpak et al. 2006, Devers et al. 2007) and limited in availability, so we used a recruitment estimate from a mixed-mesophytic forest in North Carolina as a supplemental maximum estimate (Tirpak et al. 2006). Data were lacking to define a range of values for perturbations of initial abundance and K , so we halved and doubled values of these parameters to obtain maximum and minimum values, respectively. We had no reason to expect management to affect only 1 age class, so we did not run stage-specific simulations for this analysis.

Management Simulations

To simulate population response to habitat management, we modified our spatial habitat model by adding patches of high-quality habitat (hereafter habitat units [HU]) designed to mimic areas of ruffed grouse habitat management. We modeled 8 different scenarios where we considered all possible combinations of individual HU size (large HU = 100 ha, small HU = 25 ha) and area managed (5%, 10%, 15%, and 20% of total state-controlled land area is modified). This design allowed us to directly compare the importance of large versus small patch size across a range of management effort (e.g., if 15% of the land area is devoted to management, how will population response differ if management is implemented using large vs. small patch sizes; Fig. 2). We assumed managed areas conformed to established forest management techniques known to benefit ruffed grouse and associated wildlife (e.g., Gullion 1984b, Thompson and Dessecker 1997, Storm et al. 2003), such that resulting vital rates in HU would increase relative to surrounding low-quality habitat. We assumed survival in high-quality habitat should approximate maximum values reported for the species ($S_J = 0.522$, $S_A = 0.569$; Tirpak et al. 2006). Estimates of ruffed grouse recruitment in high-quality habitat are lacking in the literature. We

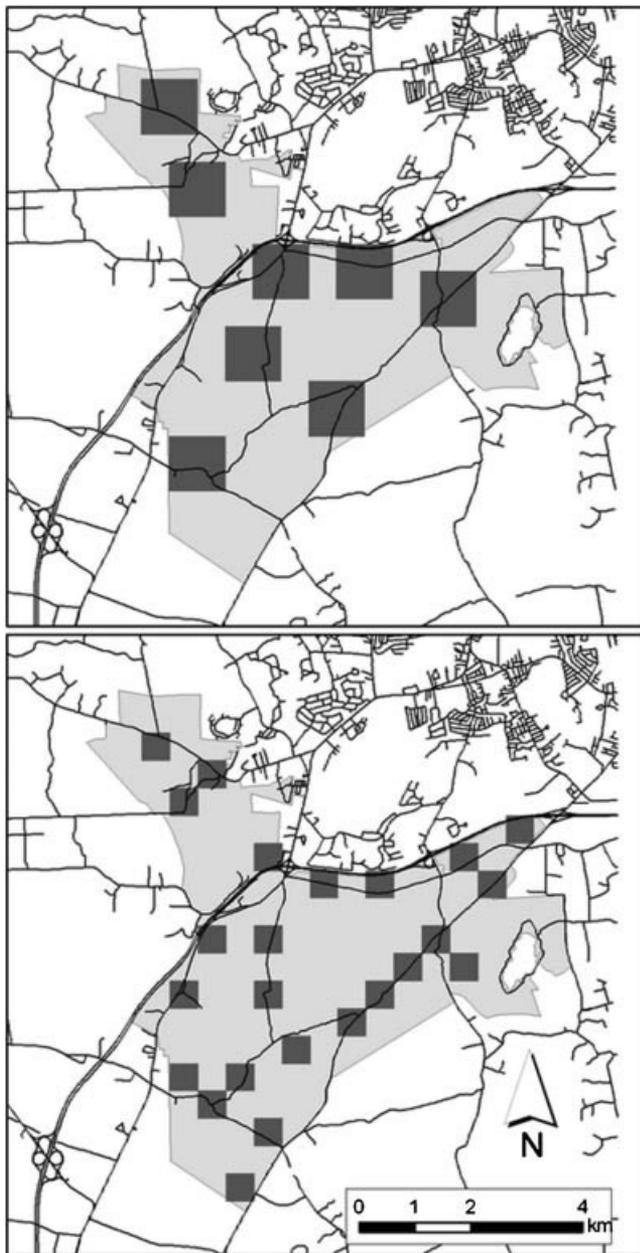


Figure 2. Example of small (bottom) and large (top) habitat units (dark squares) used to simulate ruffed grouse habitat management for a spatially explicit stochastic model of ruffed grouse population viability in southwestern Rhode Island, USA. This example depicts management on 15% of the total land area in the Big River Management Area (lightly shaded area; lines depict roads).

generated a recruitment value for management areas using a closed single population model with an initial population of 100 individuals, and systematically increased recruitment rates by 5% until the population stabilized. This resulted in recruitment estimates of 0.44 for chicks hatched by sub-adult hens and 0.48 for chicks hatched by adult hens (50% increase over baseline levels). We set carrying capacity in HU equivalent to densities observed in forests specifically managed for ruffed grouse (1 female/5 ha; Gullion 1984c, Storm et al. 2003).

We speculated that dispersing subadults would select and colonize managed areas over currently available lower quality habitat, but we lacked sufficient data to quantify the strength of this selection. We therefore conducted 2 replications of all management simulations. The first replication (hereafter original dispersal) used the same dispersal distance function described above. For the second (hereafter modified dispersal), we doubled the rate of dispersal to patches that contained HU and halved the rate of dispersal to non-managed patches.

Post hoc sensitivity analysis.—Sensitivity or elasticity analysis is often used to identify vital rates with the greatest influence on population growth; however, in some cases management may be more effectively targeted at vital rates with relatively moderate sensitivities (Caswell 2000, Reed et al. 2009). To assess the relative ability for management to influence population growth by increasing survival, recruitment, or both concomitantly, we conducted a post hoc sensitivity analysis. We systematically increased either survival or recruitment over the highest reported values for oak-hickory forests, while holding the other parameter constant, until probability of population persistence reached 1.0. Once we ran these individual vital rate simulations, we also ran all combinations of survival and recruitment within the same range of values. This allowed us to generate a continuum of predicted responses given a range of management alternatives.

Model comparisons.—We used 3 metrics for model evaluation: population rate of change (λ), median time to extinction, and probability of population persistence. RAMAS does not provide a direct estimate of λ , so we independently calculated λ for each stochastic simulation as the average growth rate based on mean predicted abundance at each time step (Tirpak et al. 2006). Our overall goal was to make predictions based on relative comparisons between models, rather than to predict an absolute value for time to extinction. So, we assessed model results based on the relative difference in λ or persistence probability among models. We present median time to extinction primarily for consistency with other studies (e.g., Tirpak et al. 2006).

RESULTS

All baseline (non-management simulation) models predicted ruffed grouse population declines throughout the 50-year simulation (Table 2). Perturbations of vital rates (survival and recruitment) caused the highest variation in model predictions, whereas perturbations of other parameters (dispersal rate and distance, initial abundance, carrying capacity) caused little to no variation (Table 2). The model was most sensitive to concomitant perturbations of survival and recruitment; λ decreased by 55% when minimum values of survival and recruitment were used for both age classes, and λ increased by 16% when maximum values were used for each parameter. In general, model results were more sensitive to inclusion of minimum parameter values compared to maximum values (Table 2). Decreasing survival and recruitment from median values caused a 26% and 28% reduction in λ , respectively, whereas increasing both parameters increased λ by 5% and 12%, respectively.

Table 2. Population rate of change (λ), median time to extinction (yr), and probability of persistence predicted by parameter perturbations of a spatially explicit stochastic model of ruffed grouse population viability in southwestern Rhode Island, USA. Parameter values used for perturbations are listed in Table 1.

Perturbation	λ (% change ^a)	Median time to extinction (% change ^a)	Probability of persistence
Min. values			
Survival and recruitment	0.37 (-55)	5.8 (-72)	0.00
Survival	0.61 (-26)	10.2 (-51)	0.00
Recruitment	0.59 (-28)	9.7 (-54)	0.00
Carrying capacity	0.83 (1)	18.1 (-13)	0.01
Dispersal	0.80 (-2)	21.6 (3)	0.01
Initial abundance	0.81 (-1)	19.0 (-9)	0.00
Median values			
All parameters	0.82 (0)	20.9 (0)	0.01
Max. values			
Dispersal	0.82 (0)	21.1 (1)	0.01
Initial abundance	0.81 (-1)	23.1 (11)	0.01
Recruitment	0.92 (12)	40.8 (95)	0.31
Carrying capacity	0.82 (0)	23.4 (12)	0.01
Survival	0.86 (5)	26.7 (28)	0.04
Survival and recruitment	0.95 (16)	^b	0.59

^a Percent change relative to model where all parameters are held at median values.

^b Population extant at end of simulation.

For all management simulations, the addition of HU increased population persistence compared to the baseline models (Table 3). When we assumed dispersing individuals would not preferentially settle managed patches, simulations with small HU resulted in slightly greater probabilities of persistence than did those with large HU, and as a greater % of state land area was modified, the increase in persistence probability was similar between these 2 sets of models (Fig. 3). When we doubled the rate of immigration to patches that contained HU and halved the rate of immigration to non-managed patches, large and small HU produced similar probabilities of persistence when 5% of state land area was manipulated, but large HU produced greater probabilities of persistence when 10%, 15%, and 20% of state land area was manipulated (Fig. 3). We achieved the greatest probability of persistence using large HU that covered 20% of state management areas, assuming increased dispersal into managed patches. Under these conditions, the probability of

persistence increased 35% (Fig. 3) compared to the baseline model with median values for all parameters (Table 3), with $\lambda = 0.94$.

Our post hoc analysis showed that a 50% increase in survival ($S \times 1.50$) over values currently reported for oak-hickory forests (adult $S = 0.85$, subadult $S = 0.78$) would result in 100% probability of population persistence (Table 4). Using the same post hoc analysis, we determined that a 100% increase in recruitment ($R \times 2.0$) would also produce stable populations (adult $R = 0.77$, subadult $R = 0.71$). Various combinations of survival and recruitment values resulted in 100% probability of persistence (Table 4).

DISCUSSION

Our models predicted general ruffed grouse decline consistent with recent trend data based on roadside surveys and fall trapping success, which indicate ruffed grouse populations

Table 3. Population rate of change (λ), median time to extinction (yr), and probability of persistence predicted by stochastic models of ruffed grouse population viability given current habitat availability (median values), and based on varying levels of simulated habitat management in southwestern Rhode Island, USA.

Simulation	Scenario	λ (% change ^a)	Median time to extinction (% change ^a)	Probability of persistence
Median values				
Large habitat units, normal dispersal	20% managed	0.90 (9)	32.3 (35)	0.15
	15% managed	0.89 (8)	29.7 (30)	0.12
	10% managed	0.89 (8)	29.7 (30)	0.09
	5% managed	0.88 (8)	28.6 (27)	0.06
	20% managed	0.94 (13)	40.1 (48)	0.36
Large habitat units, modified dispersal	15% managed	0.93 (12)	35.2 (41)	0.28
	10% managed	0.91 (10)	35.3 (41)	0.23
	5% managed	0.90 (9)	30.4 (31)	0.13
	20% managed	0.91 (10)	29.4 (29)	0.17
	15% managed	0.91 (10)	28.9 (28)	0.15
Small habitat units, normal dispersal	10% managed	0.89 (8)	26.9 (22)	0.1
	5% managed	0.88 (7)	27.3 (23)	0.07
	20% managed	0.93 (12)	30.1(44)	0.25
	15% managed	0.90 (9)	29.7(30)	0.2
	10% managed	0.91 (10)	27.8(33)	0.17
Small habitat units, modified dispersal	5% managed	0.90 (9)	28.6(37)	0.14

^a Percent change relative to model where all parameters are held at median values.

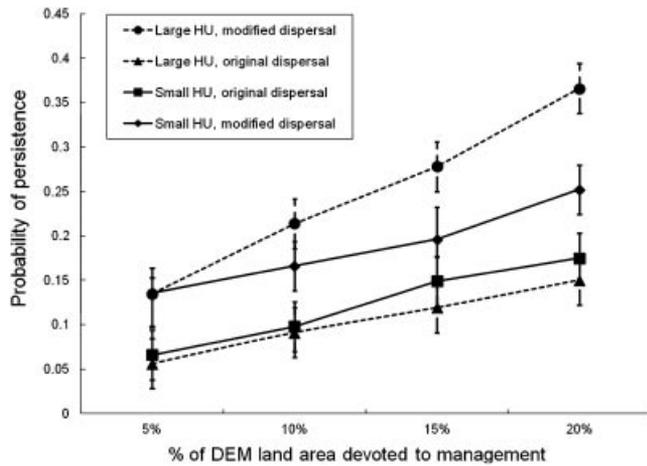


Figure 3. Probability of population persistence as predicted by stochastic simulation models of ruffed grouse population persistence in southwestern Rhode Island, USA, under different configurations of simulated habitat management and dispersal rates. The error bars represent 95% confidence intervals for each measured probability of persistence. The dotted lines represent 100 ha habitat units (large HU), whereas the solid lines represent 25 ha habitat units (small HU). An increasing amount of Department of Environmental Management (DEM) land area was modified for each simulation, as indicated on the x -axis.

are experiencing substantial declines in southern Rhode Island (Blomberg et al. 2009). Additionally, specific model estimates of λ are similar to those observed at other study sites (Tirpak et al. 2006, Devers et al. 2007). Our parameter perturbations showed that model results were most influenced by survival and recruitment, and were essentially uninfluenced by changes in carrying capacity, dispersal rate and distance, and initial abundance. Previous studies present conflicting results from sensitivity and elasticity analyses. This could be due, in part, to use of different analytic methods (Caswell 2000, Wisdom et al. 2000, Fefferman and Reed 2006). Devers et al. (2007) developed deterministic population models for the entire Appalachian region and showed that recruitment had a greater influence than survival rate on population trends. Tirpak et al. (2006) found varying degrees of sensitivity to either brood survival or adult survival, depending on specific geographic regions and forest associations. Our perturbation analysis supports the apparent importance of both vital rates to population persistence.

When interpreting perturbation analyses, it is useful to consider how efficiently management can benefit the vital rate(s) deemed to have the greatest influence on population dynamics (Reed et al. 2009). When compared to more

northern core populations, ruffed grouse survival is relatively high in the southern fringe of the species' distribution (Devers et al. 2007). This may reflect adaptation to conditions that generally favor survival and thus may limit the potential for management to further increase survival in some areas. Conversely, reproduction for southern ruffed grouse is generally low, likely because of low chick survival (Tirpak et al. 2006, Devers et al. 2007). Our post hoc sensitivity analysis determined that survival alone would need to increase by 50% to ensure population persistence, given our model. These survival rates (adult $S = 0.85$, subadult $S = 0.78$) would be substantially greater than have been previously reported for a population of ruffed grouse. In contrast, a 100% increase in recruitment represented a larger proportional increase in a vital rate, but may represent a more realistic target (increasing to adult $R = 0.77$, subadult $R = 0.71$). Realistically, managers may elect to focus on concomitantly increasing survival and recruitment, and we have provided a range of predictions given various increases in each vital rate to assist the decision making process.

Our perturbation analyses showed that models were insensitive to variation in dispersal distance and rate in a static landscape, whereas our management simulations showed that the proportion of subadults that colonized newly created HU had a major influence on population trends. The discrepancy between these 2 results may be a function of our study landscape, where existing patches may have been near enough to allow for adequate dispersal given the ruffed grouse's impressive dispersal capabilities. Small and Rusch (1989) documented that ruffed grouse readily dispersed through a heterogeneous landscape where only 30% of the land area was comprised of patchily distributed forest habitat. Working in more contiguous forest habitat Yoder (2004) and Smith (2006) documented dispersal rates and distances that were similar to those of Small and Rusch (1989), suggesting that ruffed grouse are adapted to disperse at high rates across relatively long distances regardless of landscape composition. When we simulated preferential dispersal to newly created habitat by subadults, models predicted substantial increases in probability of persistence because more individuals colonized high-quality habitats and experienced greater survival and reproduction. Our results suggest that when average inter-patch distance falls within normal ruffed grouse dispersal distances, population persistence is determined by the subsequent survival and reproduction (as determined by habitat quality) of individuals post-dispersal. Therefore, the strength at which subadult grouse select newly created

Table 4. Probabilities of persistence from a vital rate sensitivity analysis to determine the relative contributions of increased recruitment (R) and survival (S) to population growth, as estimated by stochastic models of ruffed grouse population viability. Initial vital rate values ($R \times 1$; $S \times 1$) were as follows: adult $S = 0.569$; subadult $S = 0.522$; adult $R = 0.386$; subadult $R = 0.353$.

	$R \times 1$	$R \times 1.2$	$R \times 1.4$	$R \times 1.6$	$R \times 1.8$	$R \times 2.0$
$S \times 1$	0.00	0.10	0.48	0.85	0.98	1.00
$S \times 1.1$	0.13	0.47	0.85	0.96	1.00	
$S \times 1.2$	0.52	0.89	0.98	1.00		
$S \times 1.3$	0.89	0.99	1.00			
$S \times 1.4$	0.99	1.00				
$S \times 1.5$	1.00					

high-quality habitat over pre-existing low-quality habitat has a large influence on predicted management effectiveness.

Here, we have presented the first application of spatially explicit population modeling to assess habitat management alternatives for ruffed grouse. The vital rates we used in this study span reported values for ruffed grouse, and landscape conditions, land use patterns, and disturbance regimes in our study area are representative of oak-hickory forests in the region. Therefore, our conclusions can be generalized to ruffed grouse populations inhabiting similar forests throughout the eastern and southeastern United States that are experiencing decline. Our results suggest that if larger amounts of quality ruffed grouse habitat are created in a localized area, they would provide a greater benefit to populations than many small patches distributed throughout a larger matrix of non-habitat. The question of several large versus many small reserves is a lasting controversy in the field of conservation biology, originating with the theory of island biogeography (MacArthur and Wilson 1967). Issues related to management area size are of fundamental importance to ruffed grouse, especially when placed in the broader context of the conservation of early successional forests. Many early successional forest species use smaller patches than are required by ruffed grouse, and management recommendations are often made accordingly. For example, Chandler et al. (2009) recommend a minimum patch size of 1.2 ha for managed forest openings. Although ruffed grouse will use patches of approximately this size (Gullion 1984c), they are substantially smaller than typical ruffed grouse home ranges (7.3–49.1 ha; Whitaker et al. 2007), and as such are unlikely to maximize benefits at the population level. Presumably, larger patches would not only maximize benefits to ruffed grouse but also provide adequate habitat for other early successional wildlife with smaller area requirements (e.g., shrubland songbirds, Rudnický and Hunter 1993, Lehnen and Rodewald 2009; New England cottontail rabbits [*Sylvilagus transitionalis*], Litvaitis and Villafuerte 1996; American woodcock [*Scelopax minor*], Dessecker and McAuley 2001).

We did not specify individual silvicultural treatments in this study; we merely simulated the total amount of early successional management in a discrete location (HU). Ruffed grouse require diverse forest structures to satisfy all life history requirements, such as open understories in pole-stage stands for nesting combined with dense understories in adjacent sapling-stage stands for brood rearing (Bump et al. 1947; Gullion 1984a, b; Rusch et al. 2000). Given the results of our perturbation analysis, attention should be paid to specific habitat conditions that may limit survival and recruitment. Ruffed grouse survival in the southeastern United States is probably most limited during the winter months (Devers et al. 2007). Managers should therefore conduct specific management prescriptions that increase winter food sources (Servello and Kirkpatrick 1989, Jones and Harper 2006), as well as thermal (Thompson and Fritzell 1988, Whitaker and Stauffer 2003), and escape cover (Gullion 1984b, Whitaker and Stauffer 2003, Jones and Harper 2004) to increase survival. Additionally, reproduc-

tion is likely limited by low chick survival (Tirpak et al. 2006, Devers et al. 2007) and managers should provide areas of abundant understory vegetation and high arthropod availability (Thompson et al. 1987, Hollifield and Dimmick 1995, Whitaker et al. 2006, Jones et al. 2008). We envision that carefully managed forest habitat which contains a mosaic of seral stages (Gullion 1984b; Thompson and Dessecker 1997; Storm et al. 2003; Jones and Harper 2004, 2006), within the context of a larger patch structure, will be most effective at accomplishing these goals.

Our models show the degree to which habitat management might improve conditions for ruffed grouse at a landscape scale, but even the most intense management scenarios resulted in low persistence probabilities within 50 years. However, models are simplifications of reality (Starfield 1997), and thus our results should be viewed within the context of our assumptions, and used comparatively rather than as absolute predictions of population persistence (Reed et al. 2002). Regardless, it is instructive to identify uncertainties in parameter estimates to identify information needs and to guide future research. First, we assumed that habitat management would improve ruffed grouse recruitment by a factor of 1.5. However, we may have underestimated the level of increased recruitment resulting from habitat manipulation, which in turn may have led us to underestimate population response to management. Second, the rate at which dispersing ruffed grouse find and select newly created habitat is unknown. We may have underestimated the rate at which dispersing subadults settle managed habitats, and in turn overestimated the number of individuals that settled in low-quality sink habitats. Additionally, we did not consider increased immigration from outside of the study area in response to management. Finally, the extent to which a lack of breeding partners, genetic isolation, and inbreeding effects may influence ruffed grouse populations as they decline to low levels is unknown, and could not be assessed in our models. These uncertainties demonstrate deficiencies in our current knowledge of ruffed grouse ecology that warrant further investigation. Ultimately research conducted on the ground that links specific forest management practices to population demographics is needed to answer many of these questions.

MANAGEMENT IMPLICATIONS

Ruffed grouse populations will likely continue to decline in the southern extent of their range as early successional forest habitat continues to decline in availability. In the absence of a return to historical disturbance regimes, focused forest management is necessary to provide habitat for early successional wildlife in the eastern United States (Brooks 2003, Lorimer and White 2003). Given limited resources, we recommend focusing on creating fewer large, as opposed to many small, patches of ruffed grouse habitat. We selected a somewhat arbitrary area of 100 ha for our simulations, but this size may be conceptually optimal as it encompasses the area requirements of many other taxa associated with early successional forests. Thus, 100-ha patches comprised of a carefully managed mosaic of seral stages, evenly distributed across a

landscape of interest, should maximize benefits to ruffed grouse and associated wildlife. We have focused on recommendations specific to habitat improvement, although we acknowledge other options to influence vital rates exist, such as predator control or manipulation of harvest rates (but see comments in Devers et al. 2007). We suggest our recommendations be treated as hypotheses to be empirically tested through adaptive habitat management whenever possible.

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