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Ruffed grouse population dynamics in the central and southern Appalachians

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ABSTRACT

Ruffed grouse (*Bonasa umbellus*; hereafter grouse) populations in the central and southern Appalachians are in decline. However, limited information on the dynamics of these populations prevents the development of effective management strategies to reverse these trends. We used radiotelemetry data collected on grouse to parameterize 6 models of population growth to: (1) determine the pattern of growth in these populations, and (2) identify the demographic rates most important to growth. Trend estimates from population models were most similar to trend estimates derived from Breeding Bird Survey and Christmas Bird Count data when models incorporated either a reproductive or survival event. These events randomly increased fecundity or survival, respectively, to their empirical maxima on average once every 5 years. Reproductive events improved estimates on areas dominated by mixed mesophytic forest, while survival events characterized population growth on oak (*Quercus* spp.)-dominated sites. The finite rate of increase (λ) was most sensitive to brood survival followed by adult and juvenile non-breeding survival on most sites. However, brood survival was low (<0.35 female chicks/hen survived to week 5), and elasticity analyses indicated λ responded more strongly to proportionate change in non-breeding and breeding survival rates of adults and juveniles than any reproductive variable. Life stage analyses corroborated this result. At baseline values, survival of adults and juveniles may be the main determinants of growth in these populations, and reproduction may not be adequate to compensate for these losses. Therefore, population growth above baseline levels may be

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regularly needed to restock these populations. Researchers have hypothesized that population dynamics may differ between mixed mesopytic and oak-dominated sites due to differences in forage quality and quantity. Thus, a potential mechanism for the increases in λ needed to sustain populations on mixed mesophytic forest sites is the greater fecundity observed during years with high oak or beech (*Fagus grandifolia*) mast abundance. The availability of this high quality forage allows hens to enter the breeding season in better condition and realize higher fertility. Alternatively, on oak-dominated sites, population growth increases may also be a product of higher non-breeding survival of birds in mast years, when birds do not need to range as far to forage and can limit their exposure to predators.

1. Introduction

Ruffed grouse are associated with early successional aspen (*Populus* spp.) forests across most of their North American range (Svoboda and Gullion, 1972). However, in the central and southern Appalachians (CSA), grouse are found at the periphery of this range, where aspen is sparse (Cole and Dimmick, 1991). Because grouse rely heavily on aspen as both food and cover (Rusch and Keith, 1971; Svoboda and Gullion, 1972), the absence of this preferred resource in the CSA may negatively affect the survival and reproduction of birds in this region. The historically low densities of grouse in the CSA (Bump et al., 1947) are likely due to the low forage and habitat quality associated with the lack of aspen in this region (Servello and Kirkpatrick, 1987; Hewitt and Kirkpatrick, 1997).

Recent survey data suggests CSA grouse numbers may also be experiencing steady declines not paralleled in northern areas (Dhuey, 2003; Norman, 2004; Sauer et al., 2004). Although undoubtedly linked to the loss of early successional habitat throughout the CSA (Dessecker and McAuley, 2001), the cause of the declines (e.g., increased mortality, reduced productivity) remains unknown. Understanding how grouse populations respond to habitat loss is important because large-scale creation of early successional habitat is not likely in the near future (Brooks, 2003). Habitat management efforts focused on improving the vital rates with the largest influence on population growth may potentially offset some loss in habitat by improving the quality of that remaining. However, limited information on basic grouse ecology in the southern range prevents researchers from identifying these vital rates. Most previous research on grouse occurred on populations in northern states and provinces (Bump et al., 1947; Rusch and Keith, 1971; Gullion, 1984). Extending inferences from these areas to the CSA may not be justified due to the significant regional differences in vegetation types and population structure.

These issues provided the impetus for the formation of the Appalachian Cooperative Grouse Research Project (ACGRP), a coalition of federal, state, and private organizations that collected data on radiotelemetered grouse across 12 sites in 8 states throughout the CSA from 1996–2002. The primary goals of the ACGRP included: (1) determining vital rates for the CSA grouse population, (2) identifying factors limiting grouse population growth, and (3) using this information to develop management strategies to improve CSA grouse numbers (Devers, 2004). Although initial research efforts used population models to partially fulfill these objectives, the models were coarse-grained and limited to a broad geographic scale (Devers, 2005). Thus, we constructed site-specific population models of CSA grouse to examine patterns of growth in individual populations and identify the vital rates with the greatest influence on growth rate at a finer resolution. Specifically, we assessed the utility of increasingly complex models for describing population growth on each site and determined the importance of various demographic parameters by examining their influence on λ for each population.

2. Methods

Seven study areas associated with the ACGRP were used in this study: two in Virginia, two in West Virginia, and one each in Maryland, North Carolina, and Pennsylvania (Fig. 1). These study areas represented the various land ownerships, forest types, and elevations found throughout the CSA (Tirpak, 2005). Detailed descriptions of study areas are available as follows: Haulton et al. (2003) for the Virginia sites, Dobony et al.

Fig. 1 – Map of northeastern United States showing location of 7 ruffed grouse study areas in central and southern Appalachians, 1995–2002.

(2001) for the West Virginia sites, Fecske et al. (2002) for the Maryland site, Schumacher (2002) for the North Carolina site, and Tirpak et al. (2005) for the Pennsylvania site.

Based on field experience and life history traits, we constructed a conceptual model of grouse population dynamics (Fig. 2) that included all pathways by which birds were added or lost from a closed population in a single year. From this conceptual model, we identified 12 specific demographic parameters that were biologically meaningful, potentially manageable, and fundamentally different (Table 1). We used radiotelemetry data collected by the ACGRP to estimate means and variances for these parameters.

We captured birds in lilypad traps on each site in the spring (Mar–Apr) and fall (Aug–Oct), 1995–2001 (Gullion, 1965). Annual trapping effort varied among sites, commencing on the West Virginia 1 site during 1995, on the West Virginia 2, both Virginia, and the Maryland study areas during 1996, in Pennsylvania during 1998, and finally in North Carolina in 1999. Trapping continued through 2000 on all sites except Maryland, which concluded trapping in 1999. Upon capture, we aged (juvenile or adult) and sexed birds according to standard feather criterion (Hale et al., 1954). Prior to release, each grouse was fitted with an aluminum leg band and a necklace-style radiotransmitter equipped with a mortality switch.

We used portable receivers and handheld Yagi antennae to monitor birds $\geqslant 2\times$/week. When transmitters were encountered on mortality mode, we homed in on the associated bird to determine its status. In the event of mortality, evidence was assessed to determine the cause of death and final status for the bird. We censored all birds found dead within 7 days of their initial trap date to eliminate possible capture effects, birds that died from researcher-related effects (e.g., killed in a trap or harness-induced), and birds with which contact had been lost >6 months (presumably due to battery failure or permanent emigration). We determined survival rate for each age class via Kaplan-Meier product limit estimators (Kaplan and Meier, 1958), applying the Pollock correction for staggered entry of individuals into the population (Pollock et al., 1989). We calculated survival based on weekly time steps separately for breeding (1 March–31 August) and non-breeding (1 September–28 February) periods. Delineation of these periods was based on the earliest known dates for the initiation of breeding activity in the spring and the dissolution of the brood association in the fall, respectively (Godfrey and Marshall, 1969; Servello and Kirkpatrick, 1988). Variances for

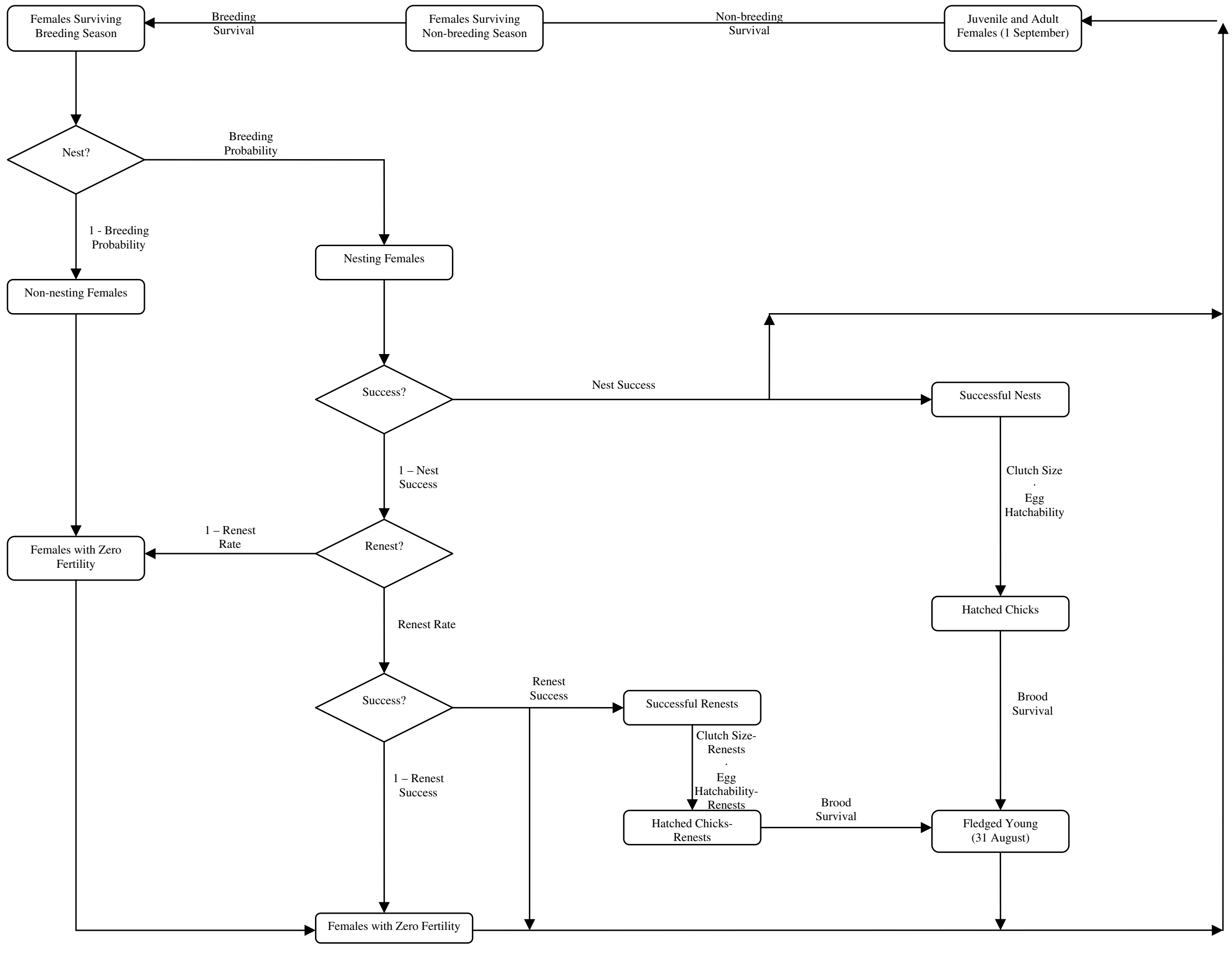

Fig. 2 – Conceptual model of ruffed grouse population growth, central and southern Appalachians, 1995–2002.

Table 1 – Definition of demographic parameters that potentially influence growth of grouse populations, central and southern Appalachians, 1995–2002

Parameter	Definition
Non-breeding survival	Survival of birds from 1 September–28 February
Breeding survival	Survival of birds from 1 March–31 August
Breeding probability	Percent hens alive on mean hatch date that attempt a nest
Nest success – first nests	Percent first nests that hatch $\geqslant 1$ egg
Clutch size – first nests	Average number of eggs/first nest
Egg hatchability – first nests	Percent of eggs hatching of those laid in ultimately successful first nests
Brood survival – first nests	Percent young alive at day 35 of those eggs that hatched in first nests
Renest rate	Percent of birds that had unsuccessful first nests and attempted a second nest
Nest success – renests	Percent second nests that hatch $\geqslant 1$ egg
Clutch size – renests	Average number of eggs/second nest
Egg hatchability – renests	Percent of eggs hatching of those laid in ultimately successful second nests
Brood survival – renests	Percent young alive at day 35 of those eggs that hatched in second nests

survival rates were estimated using the Cox and Oakes (1984) equation outlined in Pollock et al. (1989).

We monitored all females $\geqslant 3\times$/week during the laying period (Apr–May) for evidence of nesting. Birds suspected of incubating (i.e., sequentially found at the same location) were flushed to visually confirm nests. The number of eggs present was assumed to represent the final clutch size as grouse do not initiate incubation until all eggs are laid (Rusch et al., 2000). All subsequent monitoring was conducted remotely to minimize disturbance; however, when monitoring indicated a hen vacated the nest area (i.e., found repeatedly away from the nest site), we conducted a second visual inspection of the nest to determine fate (successful nests hatched $\geqslant 1$ egg) and the number of hatched eggs. We calculated nest success as the percentage of successful nests. Because nests were located shortly after initiation of incubation, this apparent nest success rate accurately reflects the success rate of nests for which incubation had been initiated (Mayfield, 1961). Within successful nests, we quantified egg hatchability as the number of laid eggs that ultimately hatched.

Unsuccessfully-nesting birds were intensively monitored for evidence of renesting through 1 July. Similar protocols were followed for these birds as for first nest attempts. Because of potentially large differences in clutch size, nest success, and egg hatchability for first and second nest attempts, we calculated these parameters independently. All birds that did not attempt a nest 1 April–1 July were considered non-breeders, and breeding probability was assessed as the percentage of hens that attempted $\geqslant 1$ nest.

Successfully-nesting hens were flushed at 1, 3, and 5 weeks posthatch (week 1 flush counts were not conducted in 2000 or 2001) to count chicks and estimate brood survival. Brood flushes were conducted by $\geqslant 2$ observers approaching the hen from opposite directions to maximize visual coverage of the brood. Using the number of hatched eggs as initial brood size, we calculated brood survival via the Flint et al. (1995) correction to the Mayfield estimator (1961) to allow for dependence among brood mates. Variance was calculated as outlined in Flint et al. (1995), with sample size equal to the number of broods. Prohibitively small sample sizes prevented calculation of a survival rate specifically for broods originating from renests. Therefore, we assumed survival was similar for chicks hatched from first and second nests and calculated brood survival on data pooled across nest attempts.

Because of large differences in habitat composition and sample size among sites, we calculated demographic parameters on a per site basis as the mean of annual estimates weighted by sample size. However, because the empirical variance of these mean estimates contained both sampling error and process variation, the variance overestimated the actual interannual variation associated with these rates (Link and Nichols, 1994). Therefore, we used a weighted variance components procedure to partition the sampling error from the total variance and accurately estimate process variation (Burnham et al., 1987). Although biologically meaningless, process variation can mathematically take on values <0, indicative of high sampling variance in parameter estimates (Gould and Nichols, 1998). To prevent underestimation of variability for parameters with a negative variance estimate, we calculated process variation as the arithmetic mean of process variation for all sites with a positive variance for that parameter. Alternatively, where no variation existed and values were fixed at 1 or 0, process variation remained undefined.

We used these estimates of demographic parameters to determine fecundity (F) and survival (S). We calculated F as the sum of the products of probabilities (and clutch size) along the two routes (first and second nest attempts) by which juveniles could be added to the population. We calculated F as a function of 11 demographic parameters:

$$F = \mathrm{nbs} * \mathrm{bs} * p * n * c * h * \mathrm{br} + \mathrm{nbs} * \mathrm{bs} * p * (1 - n) * r * n_r * c_r * h_r * \mathrm{br}$$

where nbs = non-breeding survival, bs = breeding survival, p = breeding probability, n = success of first nests, c = clutch size of first nests, h = hatchability of eggs in first nests, br = brood survival, r = renest rate, n_r = success of renests, c_r = clutch size of renests, h_r = hatchability of eggs in renests. Some nest failures and brood losses were due to hens being killed during the breeding season. Because these birds were already discounted in the breeding survival term of the fecundity equation, the empirical values of nest success and brood survival underestimate n, br, and n_r for surviving birds. Therefore, we increased these parameters by the percentage of losses due to deaths of hens – 3% for nests (Tirpak et al., 2006) and 4% for broods (ACGRP, unpublished data).

Similar to F, S summed the products of probabilities along the routes by which individuals could survive from one year to the next. We calculated S as the product of non-breeding and breeding survival:

$$S = \text{nbs} * \text{bs}$$

We used these model elements to construct separate models of grouse populations on each study site to assess how populations were growing and compare the relative influence of different vital rates on λ within and among sites. Because vital rates and population size vary with temporal and spatial scale (McArdle et al., 1990), we based all estimates on individual years and the area of the sites in this study (~4000 ha; Tirpak et al., 2006). Annual time steps reflected grouse life history, with each year beginning on 1 September, the approximate time of brood break-up and independence of chicks (Godfrey and Marshall, 1969).

We constructed all models assuming a birth-pulse population with a post-breeding census (Caswell, 2001). Because males engage in a promiscuous mating system (i.e., they potentially mate many females), provide no parental care (Rusch et al., 2000), and often outnumber females entering the breeding season (Davis and Stoll, 1973), males likely do not limit population growth. Therefore, we modeled only the female portion of the population on each site.

We constructed 6 separate models of grouse population growth to assess the utility of increasingly complex model structures for predicting λ. The first model was a basic deterministic model utilizing mean values for fecundity and survival calculated across all birds. For this model, we defined λ as N_{t+1}/N_t. We set N_0, the initial population size, to 20,000 and calculated N_{t+1}, the population size one year later, as $N_t*(F+S)$. Second, we incorporated age structure into the model to account for the potential influence of different vital rates for different aged birds on λ. Age structure was defined by 2 age classes (juveniles and adults) in a mean value Leslie matrix of model elements (Caswell, 2001). Juveniles entered adulthood immediately after their first breeding season (i.e., their second 1 September). We calculated demographic parameters and their derivative model elements independently for each age class. To ensure differences between age classes were meaningful, we compared vital rates between age classes with Z-tests for survival (Pollock et al., 1989), two-sample *t*-tests for clutch size, and χ^2 contingency tables for nest success, egg hatchability, and breeding probability. We considered tests significant at $\alpha = 0.10$ to conservatively separate adults and juveniles. The third model we constructed was a stochastic model that incorporated interannual variation in demographic rates into population growth estimates. We ran these models in RAMAS GIS (Applied Biomathematics, Setauket, NY, USA), which models environmental stochasticity by coupling the mean value matrix with a standard deviation matrix that defines distributions from which the model elements F and S are randomly drawn (Akcakaya, 2002). Although we did not have direct estimates of variability for F or S, we had estimates for the process variation associated with each component demographic parameter. Therefore, we used Monte Carlo simulations (Manly, 1997) to generate 5000 sets of demographic parameters from distributions defined by the empirical means and process variation of each demographic parameter. Although parameters have the potential to covary due to overriding effects of unmeasured intrinsic or extrinsic factors, correlations between variables were predominantly weak (<0.50), and we did not explicitly incorporate a covariance structure into these simulations. For each individual set of demographic parameters, we calculated *F* and S and the standard deviation of these model elements across all 5000 parameter sets.

We constructed the last 3 models to mimic boom events within the context of grouse population dynamics. Although drumming survey results from Virginia (Norman, 2004) and Ohio (Ohio Department of Natural Resources, 2004) suggest long-term declines in Appalachian grouse populations, these surveys also document occasional short-term increases (i.e., roughly once every 5 years the declining trend shows a spike). Because these short-term increases could be critical aspects of the population dynamics for this species, we wanted to assess the potential influence of these boom events on population growth of CSA grouse and assess whether these boom events were related to improved survival, higher reproduction, or both. Therefore, we explicitly incorporated boom years into our models as (1) random reproduction events, (2) random survival events, and (3) combinations of the two. We modeled these random events in RAMAS as “catastrophes” that had a positive effect on fecundity and survival. RAMAS models catastrophes as random events defined by two parameters: a probability of occurrence and a relative impact. We used a probability of 0.200 (i.e., an average return interval of 5 years) for these random events based on the patterns observed in the independent drumming surveys and intermediate values of mast frequency for tree species on these study areas (Fowells, 1965). We included information on mast frequency because the greater availability of high quality forage during mast years has been proposed as a mechanism for the irregular increases in grouse numbers (Devers, 2005); similar patterns have been observed in other species (Smith and Scarlett, 1987; Wolff, 1996). We limited the effects of catastrophes to the multiplicative factor that produced the maximum annual fecundity and survival values from the mean fecundity and survival values observed on each site. Although not ideal, this approach provided a consistent basis for comparison among sites and minimizes confounding environmental stochasticity, catastrophe, and study area effects. We assumed conditions favoring survival and fecundity occurred independently. Therefore, we modeled these events without an explicit covariance structure and conducted separate simulations for reproduction, survival, and combined reproduction and survival events.

For the deterministic age-structured model, we set initial populations to 10,000 for each age class and calculated λ as the dominant eigenvalue of the matrix under a stable age distribution assuming density independence. For all stochastic simulations, we projected 1000 independent populations to 500 years and calculated λ as the average annual growth rate of mean population size from these 1000 simulations. Although this procedure overestimates the true value of the stochastic growth rate (λ_S; Caswell, 2001), it provides a better comparison to the λ generated for deterministic models. The stochastic growth rate is typically calculated as the average growth rate for a long simulation (Caswell, 2001); however, because populations were declining on most sites, λ_s typically reached 0 by year 50. Because the environment at each time step was independent and drawn from an identical distribution, the average growth rate of the mean population size closely approximates the dominant eigenvalue of the mean value matrix and provides a reasonable comparison to the deterministic λ (Caswell, 2001). Additionally, we estimated median time to extinction for each stochastic model to provide a probabilistic measure of risk under each modeling scenario.

Independent data for model validation were generally not available for these sites. Therefore, we informally assessed model performance by comparing the magnitude of empirical estimates of λ from each of the 6 models to trend estimates derived from Breeding Bird Survey (BBS; Sauer et al., 2004) and Christmas Bird Count (CBC; National Audubon Society, 2002) data collected 1995–2003. Comparisons were made between an individual site and the state in which it was located, under the assumptions that trends estimated from statewide BBS and CBC data accurately reflect population growth and trends on our study areas reflect statewide trends. The relatively low detection rate for grouse, coupled with the limited number of routes and circles on which they were detected, precluded analysis at finer scales (i.e., routes or circles adjacent to study areas). To estimate BBS trends, we first determined the number of grouse detected per route per year. We restricted routes in each state to those on which grouse had been detected at least once to prevent bias associated with varying effort on routes where grouse did not occur. Additionally, we adjusted the number of routes per year to compensate for missing data (e.g., inactive or non-reporting routes). We also standardized numbers of grouse per route by the maximum annual count to express trend estimates as percentages. We then regressed these standardized counts against year and determined the trend estimate as the slope coefficient on the independent variable year. Similarly, for CBC data, we standardized the number of grouse detected per party hour and regressed these standardized counts on year to determine the trend estimate.

We performed perturbation analyses on the mean value Leslie matrix to examine the sensitivity and elasticity of λ to changes in mean values of demographic parameters (De Kroon et al., 2000). We assessed sensitivity of λ to each demographic parameter as $\Delta\lambda$ between a matrix containing mean values for each parameter and a matrix where 0.1 was added to the parameter of interest while all other parameters were held constant. Similarly, we assessed elasticity of λ to demographic parameters as $\Delta\lambda$ between a matrix containing mean values for each parameter and a matrix where the parameter of interest was increased by 10% of its mean while all other parameters were held constant. In both analyses, we assumed all sensitivities and elasticities were linear, constrained parameter values for all probabilities between 0 and 1 to avoid trivial effects, and standardized $\Delta\lambda$ by the absolute (sensitivity) or relative (elasticity) amount of perturbation to ensure meaningful comparisons among parameters. We ranked the importance of demographic parameters based on the magnitudes of the sensitivity (or elasticity) of λ to the perturbation of individual variables.

Additionally, we performed life stage analyses to determine the amount of variation in λ explained by variation in demographic parameters on each site (Wisdom et al., 2000). For each probability-based demographic parameter, we defined a β-distribution with an empirical mean and a standard deviation equal to the square root of its process error. Clutch size was similarly modeled using a normal distribution. However, process variation was negative for clutch size on all sites; therefore, we utilized the empirical standard deviation of interannual differences to define the normal curve and prevent underestimation of clutch size variance. We generated 5000 replicate sets of parameters based on independent random samples from these distributions and calculated asymptotic λ for each. We then regressed λ on each parameter to determine the amount of variation in λ explained by each parameter. Because λ is derived from these parameters, variation in λ is attributable solely to variation in these parameters. Therefore, the coefficient of determination (r^2) for each parameter represents the percentage of variability in λ explained by each parameter.

3. Results

Between 1995 and 2001, we captured 1444 grouse on the 7 study areas. Of these, 688 were females, 443 juveniles and 245 adults. Although juvenile females outnumbered adult females on all sites, the difference was greatest on the Pennsylvania site (5.059 juveniles/adult female) and least on the Virginia 2 site (1.053 juveniles/adult).

Pooling data across birds, non-breeding survival was lower than breeding survival on each site. Non-breeding survival was ~0.500 on most sites (highest on the West Virginia 2 site [0.699]), while breeding survival was >70% on most sites (lowest on the Pennsylvania study area [0.697] and highest on the West Virginia 1 site [0.830]). Annual survival ranged from 0.271 to 0.543, lowest on the Pennsylvania site and highest in West Virginia. The majority of mortalities (>80%) were directly attributable to predation; harvest-related mortality was generally low on these study areas (~12% of all mortalities) and appeared compensatory (Devers, 2005).

On all but the Virginia 2 and West Virginia 2 sites, every female attempted at least one nest. Even on these sites, breeding probability was high (95.9% and 88.7%, respectively). Across all study areas, we observed 324 known-fate first nests, allowing enumeration of 282 complete clutches containing 1 913 eggs. Renests were less common ($n = 18$) and observed on only 3 sites (Maryland, Pennsylvania, and West Virginia 1). Together, first and second nests produced 172 broods with $\geqslant 2$ complete counts. Fecundity calculated from these data varied from 0.092–0.566, lowest on the Virginia 2 site and highest on the North Carolina site. Basic deterministic models projected declining populations on all sites ($\lambda < 1.000$). Not surprisingly, λ was smallest on the Pennsylvania and Virginia 2 sites, the areas with the poorest survival and fecundity, respectively (Table 2).

Because non-breeding and breeding survival differed between age classes on at least one site (typically lower for juveniles than adults), we entered these parameters independently into all matrices. Alternatively, demographic parameters relating to fertility did not differ between age classes on any site. Therefore, we pooled reproductive data across age classes to determine fertility (Table 3).

Mean value age-specific matrices were similar across sites. Adult females exhibited higher survival and fecundity than juveniles and had higher reproductive values (Fig. 3). Stable

Table 2 – Estimates of finite rate of increase (λ) derived from 6 models of grouse population growth, central and southern Appalachians, 1995–2002

State	Model	λ	Median time to extinction (years)
Maryland	Deterministic	0.658	
	Deterministic age structure	0.665	
	Stochastic age structure	0.657	21.1
	Stochastic age structure – reproduction and survival	1.063	65.4
	Stochastic age structure – reproduction	**0.989**[a]	46.7
	Stochastic age structure – survival	0.716	25.6
North Carolina	Deterministic	0.920	
	Deterministic age structure	0.896	
	Stochastic age structure	0.885	48.3
	Stochastic age structure – reproduction and survival	1.132	465.7
	Stochastic age structure – reproduction	**1.099**	286.3
	Stochastic age structure – survival	0.913	53.5
Pennsylvania	Deterministic	0.512	
	Deterministic age structure	0.613	
	Stochastic age structure	0.595	15.6
	Stochastic age structure – reproduction and survival	**0.862**	27.7
	Stochastic age structure – reproduction	0.780	24.2
	Stochastic age structure – survival	0.654	17.1
Virginia 2	Deterministic	0.509	
	Deterministic age structure	0.569	
	Stochastic age structure	0.553	15.0
	Stochastic age structure – reproduction and survival	1.507	283.3
	Stochastic age structure – reproduction	**0.992**	25.5
	Stochastic age structure – survival	**0.995**	27.3
Virginia 3	Deterministic	0.567	
	Deterministic age structure	0.520	
	Stochastic age structure	0.510	14.9
	Stochastic age structure – reproduction and survival	1.069	29.4
	Stochastic age structure – reproduction	**1.063**	24.5
	Stochastic age structure – survival	0.555	15.2
West Virginia 1	Deterministic	0.679	
	Deterministic age structure	0.652	
	Stochastic age structure	0.650	17.6
	Stochastic age structure – reproduction and survival	2.034	–[b]
	Stochastic age structure – reproduction	**1.177**	45.5
	Stochastic age structure – survival	1.216	49.5
West Virginia 2	Deterministic	0.934	
	Deterministic age structure	0.945	
	Stochastic age structure	0.955	87.7
	Stochastic age structure – reproduction and survival	1.238	–
	Stochastic age structure – reproduction	1.206	–
	Stochastic age structure – survival	**0.992**	158.8

[a] Bold denotes model best approximating BBS and/or CBC trend.

[b] >50% of 1000 iterations did not go extinct after 500 time steps.

age distributions favored adults on all sites except North Carolina, which had the highest adult fecundity. Finite rates of increase associated with age-structured models were higher than those for simple deterministic models on 4 sites (Maryland, Pennsylvania, Virginia 3, and West Virginia 2) and lower on the other 3. All sites were characterized by declining populations (range $\lambda = 0.520–0.945$; Table 2).

Incorporating environmental stochasticity into the deterministic age-structured model resulted in a lower λ on all sites. Conversely, building either survival or reproductive events into models increased λ. Models containing both events resulted in the largest increases in λ. Inclusion of reproductive events alone increased λ more than inclusion of just survival events (Table 2).

BBS survey data suggested declines were occurring on the Maryland, Pennsylvania, and West Virginia sites; however, none of these trends were significant ($P \geqslant 0.243$). Sufficient BBS data was not available to estimate trends for North Carolina or Virginia. CBC data indicated significant declines were occurring in Maryland, Pennsylvania, and Virginia ($P \leqslant 0.050$),

Table 3 – Demographic parameter estimates, females separated by age class, central and southern Appalachians, 1995–2002

Study area	Parameter	*n*	Mean	Years	Empirical variance	Process variance	σ
Maryland	Adult non-breeding survival	30	0.478	6	0.056	0.049	0.222
	Adult breeding survival	19	0.777	6	0.050	0.030	0.174
	Juvenile non-breeding survival	80	0.458	5	0.039	0.015	0.122
	Juvenile breeding survival	34	0.792	5	0.029	0.007	0.085
	Breeding probability	36	1.000	6	0.000	–[a]	–
	Clutch size	32	11.094	6	0.700	−2.413	0.837
	Nest success	36	0.639	6	0.012	−0.014	0.051
	Egg hatchability	232	0.780	6	0.017	0.016	0.125
	Brood survival	15	0.258	4	0.002	0.001	0.024
	Renest rate	13	0.308	6	0.083	0.049	0.222
	Clutch size – renests	4	6.750	2	0.125	−0.469	0.354
	Nest success – renests	4	0.500	2	0.125	–	–
North Carolina	Adult non-breeding survival	29	0.629	3	0.039	0.021	0.144
	Adult breeding survival	19	0.667	2	0.056	0.047	0.217
	Juvenile non-breeding survival	55	0.438	3	0.025	0.015	0.122
	Juvenile breeding survival	24	0.727	3	0.023	0.019	0.138
	Breeding probability	15	1.000	2	0.000	–	–
	Clutch size	15	10.400	2	0.214	−1.564	0.463
	Nest success	15	0.875	2	0.017	0.012	0.110
	Egg hatchability	137	0.945	2	0.001	0.001	0.029
	Brood survival	12	0.348	2	0.129	0.008	0.089
	Renest rate	2	0.000	2	0.000	–	–
Pennsylvania	Adult non-breeding survival	22	0.401	4	0.020	−0.032	0.165
	Adult breeding survival	8	1.000	4	0.000	–	–
	Juvenile non-breeding survival	87	0.388	3	0.009	−0.001	0.149
	Juvenile breeding survival	34	0.618	4	0.039	0.010	0.099
	Breeding probability	61	1.000	4	0.000	–	–
	Clutch size	60	9.767	4	0.483	−1.753	0.695
	Nest success	61	0.557	4	0.039	0.038	0.195
	Egg hatchability	337	0.843	4	0.003	0.001	0.037
	Brood survival	31	0.331	4	0.002	<0.001	0.061
	Renest rate	27	0.296	4	0.039	0.011	0.103
	Clutch size – renests	8	6.667	4	2.750	2.744	1.656
	Nest success – renests	8	0.500	4	0.167	0.178	0.422
	Egg hatchability – renests	27	0.963	3	0.003	0.001	0.034
Virginia 2	Adult non-breeding survival	37	0.629	6	0.099	0.089	0.299
	Adult breeding survival	29	0.756	6	0.062	0.039	0.196
	Juvenile non-breeding survival	41	0.426	6	0.076	0.064	0.253
	Juvenile breeding survival	24	0.875	6	0.049	0.022	0.149
	Breeding probability	49	0.959	6	0.020	<0.001	0.011
	Clutch size	37	8.892	6	2.796	−1.125	1.672
	Nest success	46	0.478	6	0.055	0.032	0.179
	Egg hatchability	200	0.905	6	0.014	0.010	0.102
	Brood survival	22	0.112	5	0.003	0.001	0.029
	Renest rate	22	0.000	6	0.000	–	–
Virginia 3	Adult non-breeding survival	39	0.454	6	0.038	0.025	0.157
	Adult breeding survival	27	0.847	6	0.019	0.011	0.104
	Juvenile non-breeding survival	55	0.510	5	0.039	0.020	0.141
	Juvenile breeding survival	33	0.655	6	0.029	0.021	0.143
	Breeding probability	36	1.000	6	0.000	–	–
	Clutch size	33	10.091	6	1.363	−2.079	1.168
	Nest success	36	0.750	6	0.045	0.032	0.178
	Egg hatchability	265	0.894	6	0.002	−0.002	0.070
	Brood survival	24	0.155	6	0.000	0.000	0.029
	Renest rate	9	0.000	4	0.000	–	–
West Virginia 1	Adult non-breeding survival	60	0.618	6	0.063	0.044	0.209
	Adult breeding survival	58	0.759	6	0.006	−0.022	0.165
	Juvenile non-breeding survival	74	0.436	6	0.059	0.048	0.219
	Juvenile breeding survival	47	0.914	6	0.011	0.005	0.074

(*continued on next page*)

Table 3 – *continued*

Study area	Parameter	n	Mean	Years	Empirical variance	Process variance	σ
	Breeding probability	92	1.000	6	0.000	–	–
	Clutch size	80	10.188	6	0.989	−1.498	0.995
	Nest success	88	0.716	6	0.006	−0.005	0.140
	Egg hatchability	583	0.940	6	0.006	0.004	0.064
	Brood survival	50	0.152	6	0.003	0.000	0.015
	Renest rate	22	0.273	6	0.017	0.013	0.115
	Clutch size – renests	5	7.600	4	2.896	2.896	1.702
	Nest success – renests	6	0.500	5	0.250	0.020	0.140
	Egg hatchability – renests	3	1.000	3	0.000	–	–
West Virginia 2	Adult non-breeding survival	53	0.677	6	0.039	0.033	0.181
	Adult breeding survival	45	0.841	6	0.017	0.009	0.094
	Juvenile non-breeding survival	59	0.723	6	0.034	0.022	0.149
	Juvenile breeding survival	51	0.721	6	0.026	−0.001	0.119
	Breeding probability	62	0.887	5	0.013	0.007	0.086
	Clutch size	25	9.120	4	2.056	−1.130	1.434
	Nest success	42	0.643	5	0.024	0.001	0.031
	Egg hatchability	159	0.811	4	0.006	0.000	0.003
	Brood survival	18	0.319	4	0.002	0.000	0.021
	Renest rate	15	0.000	5	0.000	–	–

a Undefined.

while small (<1%/year) increases were observed in North Carolina and West Virginia. However, trends on these latter sites were not significant ($P \geqslant 0.840$; Table 4).

The three most basic models of grouse population growth poorly estimated BBS and CBC trends. Estimates of λ from models combining data across age classes differed widely. Incorporating age structure or environmental stochasticity only mildly improved agreement between model and survey results (Table 2).

Alternatively, models incorporating random increases in reproduction and survival were more closely aligned with the statewide survey trend estimates. However, the best model varied among sites. On the Maryland, Virginia, and West Virginia 1 study areas, models incorporating only reproductive events were best, on the West Virginia 2 site survival alone was best, and on the Pennsylvania and North Carolina sites reproduction and survival events together best approximated BBS and CBC trends (Table 2).

On the majority of sites, λ was most sensitive to brood survival followed by non-breeding survival of juveniles and adults (Table 5). Indeed, these 3 were the most important parameters in terms of sensitivity on all sites. In particular, brood survival dominated all but the Pennsylvania study area. The finite rate of increase responded secondarily to adult and juvenile breeding survival as well as nest success, with these parameters generally the fourth or fifth most important on most sites.

On 6 sites, λ was most elastic to adult non-breeding survival (Table 5). On 5 of these sites, adult breeding survival exerted an equally strong influence. These 5 sites were also similar regarding the elasticity of λ to juvenile breeding and non-breeding survival, the demographic parameters with the second-greatest effect on λ. However, on the Maryland and West Virginia 1 sites, brood survival alone was the parameter with the next greatest effect on λ, whereas on the other 3 sites all fertility variables were equally influential. Pennsylvania differed from the other study areas in the elasticity of λ to demographic parameters. Although λ was again most elastic to adult non-breeding survival, this parameter was followed by clutch size, egg hatchability, and brood survival. North Carolina was unique among sites as brood survival, nest success, and egg hatchability were had a greater influence on λ than either adult non-breeding or breeding survival.

Adult non-breeding survival also accounted for the greatest amount of variation in λ on most sites, as revealed by life stage analyses of mean value matrices (Table 6). Other strong determinants included adult breeding survival, juvenile non-breeding survival, clutch size, and nest success. Variation in all other variables was weakly related to the variation in λ ($r^2 \leqslant 0.096$). In particular, brood survival was a poor determinant ($r^2 \leqslant 0.053$), as were all parameters related to second nests ($r^2 \leqslant 0.017$).

4. Discussion

Survival rates differed between juveniles and adults and between non-breeding and breeding seasons, patterns observed in other studies (Small et al., 1991; Clark, 2000; Gutierrez et al., 2003). Differences in age-specific mortality may be associated with greater exposure to predators due to dispersal or general unfamiliarity of juveniles with the habitat within their home range (Small et al., 1993; Tirpak, 2005). Alternatively, we observed no difference in fertility estimates between age classes. Studies of other grouse species have observed differences between age classes, particularly in clutch size (Reynolds, 1997; Hannon and Smith, 1984); however, this pattern did not exist in all species (Schroeder, 1997) and has not been observed in ruffed grouse (Small et al., 1996; Devers, 2005). The relatively short lifespan of grouse may produce a strong selection pressure to maximize fertility at a young age, resulting in little difference between age classes (Murray, 1991).

ai)

$$L = \begin{pmatrix} 0.293 & 0.300 \\ 0.362 & 0.372 \end{pmatrix}$$

aii)

$$SD = \begin{pmatrix} 0.107 & 0.172 \\ 0.107 & 0.195 \end{pmatrix}$$

aiii)

$$w = \begin{pmatrix} 0.447 \\ 0.553 \end{pmatrix}$$

aiv)

$$v = \begin{pmatrix} 1.000 \\ 1.025 \end{pmatrix}$$

bi)

$$L = \begin{pmatrix} 0.476 & 0.627 \\ 0.318 & 0.419 \end{pmatrix}$$

bii)

$$SD = \begin{pmatrix} 0.231 & 0.348 \\ 0.107 & 0.173 \end{pmatrix}$$

biii)

$$w = \begin{pmatrix} 0.599 \\ 0.401 \end{pmatrix}$$

biv)

$$v = \begin{pmatrix} 1.000 \\ 1.317 \end{pmatrix}$$

ci)

$$L = \begin{pmatrix} 0.212 & 0.355 \\ 0.240 & 0.401 \end{pmatrix}$$

cii)

$$SD = \begin{pmatrix} 0.172 & 0.199 \\ 0.114 & 0.166 \end{pmatrix}$$

ciii)

$$w = \begin{pmatrix} 0.469 \\ 0.531 \end{pmatrix}$$

civ)

$$v = \begin{pmatrix} 1.000 \\ 1.673 \end{pmatrix}$$

di)

$$L = \begin{pmatrix} 0.093 & 0.119 \\ 0.373 & 0.476 \end{pmatrix}$$

dii)

$$SD = \begin{pmatrix} 0.073 & 0.085 \\ 0.230 & 0.262 \end{pmatrix}$$

diii)

$$w = \begin{pmatrix} 0.200 \\ 0.800 \end{pmatrix}$$

div)

$$v = \begin{pmatrix} 1.000 \\ 1.276 \end{pmatrix}$$

ei)

$$L = \begin{pmatrix} 0.135 & 0.156 \\ 0.334 & 0.385 \end{pmatrix}$$

eii)

$$SD = \begin{pmatrix} 0.087 & 0.089 \\ 0.129 & 0.143 \end{pmatrix}$$

eiii)

$$w = \begin{pmatrix} 0.288 \\ 0.712 \end{pmatrix}$$

eiv)

$$v = \begin{pmatrix} 1.000 \\ 1.150 \end{pmatrix}$$

fi)

$$L = \begin{pmatrix} 0.183 & 0.216 \\ 0.398 & 0.469 \end{pmatrix}$$

fii)

$$SD = \begin{pmatrix} 0.114 & 0.107 \\ 0.209 & 0.190 \end{pmatrix}$$

fiii)

$$w = \begin{pmatrix} 0.315 \\ 0.685 \end{pmatrix}$$

fiv)

$$v = \begin{pmatrix} 1.000 \\ 1.178 \end{pmatrix}$$

gi)

$$L = \begin{pmatrix} 0.376 & 0.410 \\ 0.522 & 0.569 \end{pmatrix}$$

gii)

$$SD = \begin{pmatrix} 0.128 & 0.148 \\ 0.138 & 0.167 \end{pmatrix}$$

giii)

$$w = \begin{pmatrix} 0.419 \\ 0.581 \end{pmatrix}$$

giv)

$$v = \begin{pmatrix} 1.000 \\ 1.091 \end{pmatrix}$$

Fig. 3 – Mean value matrices (i), standard deviation matrices (ii), stable age distributions (iii), and reproductive values standardized to juveniles (iv) for the Maryland (a), North Carolina (b), Pennsylvania (c), Virginia 2 (d), Virginia 3 (e), West Virginia 1 (f), and West Virginia 2 (g) study areas, central and southern Appalachians, 1995–2002.

Projections based on models developed from radiotelemetry data and statewide BBS and CBC trend estimates all indicated these populations were declining. However, the magnitude of the declines was overestimated by radiotelemetry data, particularly for the 3 most basic models. Agreement between the 3 models incorporating reproduction or survival events was often better, but still typically overestimated declines.

The discrepancy between these estimates likely resulted from many factors. The methods used to determine vital rates (particularly brood survival; Godfrey, 1975), problems associated with BBS and CBC data (e.g., variation in detection probabilities; Butcher et al., 1990), and the use of statewide estimates to reflect individual study areas could all potentially bias trend estimates. However, the effect of these confounding factors is likely minimal, and underestimation of survey trends by the 3 most basic models likely reflects their inadequate portrayal of grouse population dynamics on these sites rather than an artifact of methodology or statistical assumptions (Tirpak, 2005). Conversely, the closer agreement of models containing either reproductive or survival events with BBS and CBC survey results belies the importance of these events in CSA grouse population dynamics.

Grouse are a typical r-selected species. They occupy ephemeral habitats and have a high biotic potential; therefore, they track environmental change well. However, grouse populations in the CSA do not exhibit years of precipitous decline typical of grouse populations in northern landscapes at the ebb of the cycle (Rusch, 1989; Williams et al., 2004). Instead,

Table 4 – Trends estimated from Breeding Bird Survey and Christmas Bird Count data, central and southern Appalachians, 1995–2003

State	Breeding Bird Survey		Christmas Bird Count	
	Trend	*P*[a]	Trend	*P*[a]
Maryland	0.940	0.0243	0.921	0.050
North Carolina	–[b]	–	1.001	0.840
Pennsylvania	0.967	0.355	0.945	0.009
Virginia	–	–	0.927	0.048
West Virginia	0.990	0.328	1.004	0.879

a *n* = number of years (9).
b Insufficient data for trend estimation.

Table 5 – Sensitivity of λ to demographic parameters ranked by the magnitude of the sensitivity, central and southern Appalachians, 1995–2002

Parameter	Maryland		North Carolina		Pennsylvania		Virginia 2	
	Sensitivity	Elasticity	Sensitivity	Elasticity	Sensitivity	Elasticity	Sensitivity	Elasticity
Adult non-breeding survival	0.703	**0.134**[a]	0.832	0.137	**0.942**	**0.193**	0.472	**0.187**
Adult breeding survival	0.432	**0.134**	0.784	0.137	–	–	0.393	**0.187**
Juvenile non-breeding survival	0.716	0.131	0.907	0.104	0.583	0.116	0.547	0.147
Juvenile breeding survival	0.414	0.131	0.546	0.104	0.365	0.116	0.266	0.147
Breeding probability	–[b]	–	–	–	–	–	0.110	0.067
Clutch size	0.025	0.112	0.053	**0.144**	0.027	0.133	0.012	0.067
Nest success	0.378	0.100	0.631	**0.144**	0.400	0.117	0.190	0.067
Egg hatchability	0.360	0.112	0.584	0.084	0.309	0.133	0.117	0.067
Brood survival	**1.105**	0.119	**1.586**	**0.144**	0.823	0.145	**0.912**	0.067
Renest rate	0.053	0.007	–	–	0.078	0.012	–	–
Clutch size(2)	0.002	0.007			0.003	0.012		
Nest success(2)	0.032	0.007			0.045	0.012		
Egg hatchability(2)	0.018	0.007			0.024	0.012		

Parameter	Virginia 3		West Virginia 1		West Virginia 2	
	Sensitivity	Elasticity	Sensitivity	Elasticity	Sensitivity	Elasticity
Adult non-breeding survival	0.595	**0.170**	0.554	**0.168**	0.723	**0.127**
Adult breeding survival	0.319	**0.170**	0.451	**0.168**	0.582	**0.127**
Juvenile non-breeding survival	0.461	0.147	0.667	0.142	0.621	0.117
Juvenile breeding survival	0.358	0.147	0.274	0.142	0.622	0.117
Breeding probability	–	–	–	–	0.443	0.102
Clutch size	0.014	0.091	0.018	0.090	0.043	0.102
Nest success	0.261	0.091	0.292	0.080	0.593	0.102
Egg hatchability	0.163	0.091	0.195	0.090	0.484	0.102
Brood survival	**0.904**	0.091	**1.260**	0.098	**1.185**	0.102
Renest rate	–	–	0.059	0.008	–	–
Clutch size(2)			0.002	0.008		
Nest success(2)			0.031	0.008		
Egg hatchability(2)			–	–		

a Bold denotes demographic parameter to which λ is most sensitive or elastic.
b No variation.

population growth rates in the CSA may have lower thresholds maintained through intra- and interspecific interactions. Mean values of *F* and *S* were more similar to the empirical minima than maxima of observed values on most sites. This pattern suggests baseline reproduction and survival were typically low and CSA grouse populations were declining in most years. Therefore, over the long term, these populations likely rely on the high reproduction and survival achieved during boom years to restock their dwindling numbers.

A potential mechanism for these irregular increases in reproduction and survival was suggested by Devers (2005) and Whitaker (2003). Both observed strong effects of mast crops, particularly oak and beech, on habitat selection, home range size, reproductive performance, and survival. While birds in northern landscapes have a reliable source of food in aspen buds, birds in the CSA are more reliant on soft and hard mast crops (Servello and Kirkpatrick, 1987). In non-mast years, these resources are depleted quickly and grouse are

Table 6 – Coefficients of determination (r^2) derived from regressions of finite population growth rate on demographic parameters, central and southern Appalachians, 1995–2002

Parameter	Maryland	North Carolina	Pennsylvania	Virginia 2	Virginia 3	West Virginia 1	West Virginia 2
Adult non-breeding survival	**0.416**	0.165	**0.493**	**0.618**	**0.588**	**0.514**	**0.498**
Adult breeding survival	0.127	0.215	–	0.256	0.075	0.193	0.094
Juvenile non-breeding survival	0.157	**0.315**	0.099	0.035	0.051	0.146	0.101
Juvenile breeding survival	0.035	0.096	0.062	0.003	0.040	0.005	0.064
Breeding probability	–[a]	–	–	<0.001	–	–	0.020
Clutch size	0.112	0.060	0.062	0.011	0.073	0.021	0.183
Nest success	0.015	0.063	0.255	0.010	0.087	0.033	0.006
Egg hatchability	0.082	0.004	0.001	0.001	0.001	0.004	<0.001
Brood survival	<0.001	0.053	0.035	0.012	0.034	0.036	0.002
Renest rate	0.006	–	0.002	–	–	0.001	–
Clutch size(2)	<0.001		<0.001			<0.001	
Nest success(2)	<0.001		0.017			<0.001	
Egg hatchability(2)	0.001		0.001			–	

a Variance undefined.

b Demographic parameter with the greatest influence on λ.

sustained by low-quality foods such as mountain laurel (*Kalmia latifolia*) and Christmas fern (*Polystichum acrostichoides*; Norman and Kirkpatrick, 1984; Servello and Kirkpatrick, 1987). Foraging times for this low quality diet are high, increasing the susceptibility of birds to predators and reducing survival (Hewitt and Kirkpatrick, 1997; Jakubas and Gullion, 1991). For hens that survive to the breeding season, this low quality diet leads to poor condition, which negatively affects clutch size, egg hatchability, and brood survival (Beckerton and Middleton, 1982). Alternatively, in mast years, the abundance of high quality food allows grouse to reduce foraging times, resulting in higher survival, better condition entering the breeding season, and ultimately improved fertility (Long et al., 2004). Observed variation in vital rates corroborates this hypothesis; empirical maxima in survival and reproduction were most commonly observed in the fall of mast years and the following spring.

Sites differed in terms of which combination of survival and reproductive events best predicted BBS and CBC trend estimates. Differences among these sites likely relate to the forest composition dominant on these study areas. Mixed mesophytic species (birch [*Betula* spp.], cherry [*Prunus* spp.], and maple [*Acer* spp.]) were the primary trees on most sites (Maryland, North Carolina, Pennsylvania, Virginia 3, and West Virginia 1; J. Tirpak, unpublished data). These forests provide a diverse base of forage species in non-mast years, and these sites were typically best described by reproductive events alone. Alternatively, the oak-dominated Virginia 2 and West Virginia 2 sites were depauperate in forage species other than oak or beech (J. Tirpak, unpublished data). Population growth on these sites was described equally as well (Virginia 2) or better (West Virginia 2) by models that incorporated survival events alone. The broad forage base on the mixed mesophytic sites permits birds to survive the winter in all years; however, hens may enter the breeding season following non-mast years in poorer condition than in mast years and subsequently have poorer fertility rates (Long et al., 2004). Therefore, increased mast would likely manifest as increased fertility. Alternatively, on oak sites, the forage base is generally poor and survival in non-mast years may be lower as birds range widely for the few acorns available. Tirpak (2005) observed this on the West Virginia 2 site, where longevity of adult females was lower in home ranges that contained a higher proportion of oak forest. Birds that survive on oak-dominated sites may enter the breeding condition in good condition if they have been feeding on high-quality acorns throughout the non-breeding season. Consequently, their fertility may be high even in poor mast years. Thus, increased mast availability may manifest as increased survival for some birds on these sites. Nevertheless, due to limited resources in non-mast years, some birds may exhaust their energy reserves solely on metabolic activities associated with survival. Although these birds may live to the breeding season, they may forgo breeding (females failed to breed only on the oak-dominated sites) or have limited reproductive output in non-mast years (Devers, 2005). Thus, increased mast may also manifest as increased fertility for some birds on these sites. Thus, the influence of mast may be equally important for reproduction and survival in these contexts. The Virginia 2 site in this study exhibited this pattern.

All age-structured models were variations on the mean value matrix; therefore, we based all perturbation analyses on this matrix. The extreme sensitivity of λ to brood survival was not surprising. Reproductive events appear to be important components of grouse dynamics on these sites. Additionally, Devers (2005) found brood survival to have the greatest impact on grouse population growth in this region. Bump et al. (1947) also observed strong correlations between brood survival and fall population size in New York. However, brood survival was the demographic rate with the smallest magnitude. Therefore, adding 0.1 to these estimates represented a proportionately larger change in this parameter than that for any other variable. When proportional change was incorporated in elasticity analyses, brood survival was reduced behind breeding and non-breeding survival. A similar pattern was observed in life stage analyses. Therefore, brood survival has the greatest potential to affect λ, but at the mean rates we observed for this demographic parameter in this study, it does not.

At baseline values, survival may be more important than reproduction on most sites. In northern areas, higher numbers of chicks produced during the breeding season often equate with lower juvenile non-breeding survival during the winter (Bump et al., 1947; Chambers and Sharp, 1958). Similarly, increases in nest success do not consistently improve fall or spring population sizes (Hewitt et al., 2001). These patterns led Rusch (1989) to conclude fluctuations in fall numbers and age ratios are not related to changes in reproduction. However, we did not observe these same negative correlations on our study areas. The number of juveniles and the overall number of grouse in CSA populations rarely rivals that observed in northern populations, even during cyclic lows (Bump et al., 1947). At these low densities, even relatively large increases in juveniles may not be enough to elicit a strong density-dependent response within the population or a strong functional response in any single predator (Brown, 1969). This may explain how reproductive events can strongly influence these populations, which at average rates are more strongly impacted by changes in survival, as demonstrated by elasticity and life stage analyses.

In the CSA, the effect of survival on λ differs from northern areas. Traditionally, non-breeding survival of juveniles has been considered the primary factor driving population change in grouse (Rusch and Keith, 1971; Moss and Watson, 2001). However, we observed λ to be most sensitive to adult non-breeding survival. The reason for this shift in the relative effect of age-specific mortality on population growth rates likely related to the lower fertility and greater survival of grouse in the CSA compared to northern regions. In this study, the lowest annual survival rates were for juveniles on the Pennsylvania (0.240) and North Carolina (0.318) sites. Adult survival was considerably larger (0.401 and 0.419, respectively). In Minnesota, annual survival of female grouse is only 0.111 ± 0.082 (Gutierrez et al., 2003). The highest survival rate observed for grouse in Wisconsin is 0.33, for adults on private land; public land estimates are much lower (0.07; Small et al., 1991).

Differences in fertility among regions were mainly associated with the low brood survival in the CSA. The highest 5-week posthatch brood survival rate observed in this study was 0.348 on the North Carolina site, with brood survival substantially lower on many sites. In comparison, brood survival is 0.51 in Alberta (Rusch and Keith, 1971), 0.50 in Minnesota (Godfrey, 1975), and 0.40 in New York (Bump et al., 1947) for longer 7–12 week brood periods. Larson et al. (2001) radiocollared chicks in Michigan to estimate brood survival and calculated a rate similar to the one observed in this study (0.285–0.318). However, collars may reduce survival of chicks and a similar effort by the ACGRP also resulted in lower brood survival estimates (0.06–0.21; Smith et al., 2004).

Based on these rates, a greater number of juveniles are produced per female each year in northern regions. With juveniles outnumbering adults as much as 4:1 (Kubisiak, 1985), changes in juvenile survival may more quickly affect the population's average growth rate and size than changes in adult survival. Alternatively, in the CSA, stable age distributions favor adults, and we observed less than a single juvenile female being produced per adult female per year on many sites. However, the longevity of adults in this region may allow these birds to have similar lifetime fitness to birds in northern regions. Therefore, mortality of adult females in the CSA results in a lower average fitness for the population and a more rapid decline in population size.

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