

**Population ecology of and the effects of hunting on ruffed grouse
(*Bonasa umbellus*) in the southern and central Appalachians**

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ABSTRACT

I investigated ruffed grouse (*Bonasa umbellus*) population ecology in the southern and central Appalachians as part of the Appalachian Cooperative Grouse Research Project (ACGRP). Several hypotheses have been offered to explain the low abundance of ruffed grouse in the region including inadequate quantity of early-successional forests due to changes in land use, additive harvest mortality, low productivity and recruitment, and nutritional stress. Through the cooperative nature of the ACGRP, researchers tracked >3,000 ruffed grouse between October 1996 and September 2002 and gathered data on reproduction, recruitment, survival, and mortality factors. As part of the ACGRP my objectives were (1) estimate reproductive rates, (2) estimate survival and cause-specific mortality rates, (3) determine if ruffed grouse harvest in the Appalachian region is compensatory, and (4) estimate ruffed grouse finite population growth.

Ruffed grouse population dynamics in the Appalachian region differed greatly from the core of ruffed grouse range. In general, ruffed grouse in the Appalachian region had lower productivity and recruitment, but higher survival than reported for populations in the Great Lakes and southern Canada. However, within the southern and central Appalachian region, ruffed grouse population dynamics differed between oak-hickory and mixed-mesophytic forest associations. Productivity and recruitment

were lower in oak-hickory forests, but adult survival was higher than in mixed-mesophytic forests. Furthermore, ruffed grouse productivity and recruitment were more strongly related to hard mast (i.e., acorn) production in oak-hickory forests than in mixed-mesophytic forests. The leading cause of ruffed grouse mortality was avian predation (44% of known mortalities). Harvest mortality accounted for only 12% of all known mortalities and appeared to be compensatory. Population models indicate ruffed grouse populations in the Appalachian region are declining, but estimates vary greatly stressing the need for improved understanding of annual productivity and recruitment. We posit ruffed grouse in the Appalachian region exhibit a clinal population structure and changes in life-history strategies due to gradual changes in the quality of food resources, changes in snow fall and accumulation patterns, and predator communities. Recommendations are presented for habitat and harvest management and future research and management needs.

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Wildlife conservation programs commonly are implemented at the population level (Krebs 1994, Murphy and Noon 1991) and thus require an understanding of species population dynamics. Assessing population dynamics allows researchers and managers to elucidate ecological relationships, follow trends in abundance, set harvest regulations, and evaluate the effects of management activities on populations (Stauffer 1993, Krebs 1994). Two central concepts in population dynamics are compensatory and additive mortality hypotheses (Krebs 1994). Compensatory mortality is an important concept to understanding population regulation in non-exploited populations (Krebs 1994). The compensatory mortality hypothesis states the magnitude of each mortality factor acting upon a population may vary, but total mortality remains constant (Bailey 1984). This hypothesis forms the foundation for management of regulated sport hunting throughout the United States (Strickland et al. 1994) and assumes human harvest of populations replaces 1 or more natural mortality factors (e.g., predation) without reducing the breeding population. In contrast, under the additive mortality hypothesis, it is assumed each death adds to total mortality and reduces population size (Krebs 1994). An intermediate hypothesis between total compensation and total additivity is that harvest is compensatory up to a threshold, above which it becomes additive (Anderson and Burnham 1976). Determining whether harvest is compensatory or additive is crucial in evaluating the effects of hunting on populations (Myrberget 1985) and can be accomplished through manipulative experiments in which total losses are measured with and without harvest (Krebs 1994).

The ruffed grouse (*Bonasa umbellus*) is a popular gamebird distributed from Alaska across central and southern Canada and the northern United States to the

Atlantic Coast, south into the central Rocky Mountains and Appalachian Mountains. Its distribution coincides closely with that of aspen (*Populus tremuloides*), except in the central and southern Appalachians (Fig. 1). Current knowledge of ruffed grouse ecology and management is based primarily on research conducted in the northern United States and Canada (e.g., Bump et al. 1947, Dorney and Kabat 1960, Gullion and Marshall 1968, Gullion 1970, Gullion 1984). Presently, there is a paucity of knowledge of ruffed grouse ecology in the Appalachian region (Hein 1970, Rusch et al. 2000); data collected as part of the USGS breeding bird survey show a significant decline (-5.0 % population change/year, $P = 0.05$, $n = 56$ routes; Sauer et al. 2004) of ruffed grouse population indices in the Appalachians over the last 3 decades. The Appalachian Cooperative Grouse Research Project (ACGRP) was initiated in 1996 to investigate the apparent decline of ruffed grouse in the Appalachian Mountains.

Across its range, ruffed grouse prefer early-successional deciduous forests with high woody stem densities, dense woody cover, and dense herbaceous understory (Bump et al. 1947, Edminster 1947, Kubisiak 1985, Johnsgard 1983, Thompson et al. 1987, White and Dimmick 1978). In contrast to these broad generalizations, differences exist between grouse habitat and environmental conditions in the core of the species range (i.e., northern United States and Canada) and the Appalachian region where aspen and other high quality, easily accessible food resources are lacking.

In the core of ruffed grouse range, aspen provides cover and food and is considered the most important component of ruffed grouse habitat, but aspen is rare or nonexistent in the Appalachian region (Svoboda and Gullion 1972, Thompson and Fritzell 1988). In the core of ruffed grouse range optimal drumming and winter cover

are provided by young aspen stands with 14,000 – 20,000 stems/ha (Thompson and Fritzell 1988). Aspen stands commonly have moderately dense shrub and herbaceous layers that provide high quality brood cover (Svoboda and Gullion 1972). Aspen is also an important food source for ruffed grouse, particularly during the winter and pre-breeding periods when ruffed grouse feed primarily on aspen catkins (Servello and Kirkpatrick 1987). Early-successional hardwood forests interspersed with conifers, rhododendron (*Rhododendron* spp.), and mountain laurel (*Kalmia latifolia*) replace aspen as cover in the Appalachian region (Stafford and Dimmick 1979). Early-successional forests in the Appalachian region may provide less protection from raptors (Hein 1970) and lower quality forage (Servello and Kirkpatrick 1987) than the aspen-dominated stands of the northern United States and Canada.

In the core of their range, ruffed grouse conserve energy by snow roosting and may roost 19 – 23 hours per day (Gullion 1970, Gullion and Svoboda 1972, Ott 1990). Snow roosting reduces the energetic demands of grouse by trapping warm air near the body and reducing convectional heat loss. In northern United States and Canada, winter snow conditions, particularly dry powder snow, may afford the highest quality roosting conditions for ruffed grouse, and is correlated positively with productivity the following spring (Gullion 1970, Thompson and Fritzell 1988). Additionally, the decreased metabolic demands associated with snow roosting reduces the time spent foraging and exposure to predators (Doerr et al. 1974). In the Appalachian region snow accumulation is rarely sufficient to allow grouse to snow roost. Ruffed grouse in the southern range roost in dense coniferous cover to minimize energy demands (Thompson and Fritzell 1988, Gullion 1990). Roosting in or under eastern red cedar

(*Juniperus virginiana*) allowed ruffed grouse to reduce energy loss by 18%, 4-fold more than roosting in deciduous cover, but only slightly more than half of the savings of snow roosting (Thompson and Fritzell 1988). However, Whitaker (2003) found grouse in the Appalachian region almost invariably ground roosted when snow was present despite not being able to completely burrow beneath the snow. When snow was absent, grouse did not exhibit preference for specific roost microsites, but roosted in and under deciduous and evergreen trees and shrubs, brush piles, and leaf litter (Whitaker 2003). Whitaker (2003) hypothesized the apparent lack of preference for coniferous trees was due to the availability of fallen oak (*Quercus* spp.) leaves which may provide good thermal cover and concealment from predators. The decrease in energy savings due the lack of snow roosting increases energy demands in a region where grouse must spend a greater amount of time foraging on low quality food, thus possibly increasing predation risk (Hein 1970).

The availability of food resources to individuals and the quality of the food resources influence multiple aspects of avian reproduction and recruitment including clutch size, egg quality, incubation date, and chick survival (Nager et al. 2000, Reynolds et al. 2003, Verboven et al. 2003). The nutritional quality of ruffed grouse diets differ markedly between the core and Appalachian regions. Throughout most of their range grouse depend on aspen (i.e., buds, twigs, and catkins) to meet their nutritional requirements (Svoboda and Gullion 1972, Servello and Kirkpatrick 1987, Hewitt and Kirkpatrick 1996). Ruffed grouse diets in the Appalachian region consist of the leaves and seeds of herbaceous plants, oak nuts, buds and nuts of beech (*Fagus grandifolia*), birch (*Betula* spp.), and cherry trees (*Prunus* spp.), leaves of evergreen species

including mountain laurel and great rhododendron (*R. maximum*), and fruit of greenbrier (*Smilax spp.*) and grape (*Vitis spp.*; Bump et al. 1947, Stafford and Dimmick 1979, Servello and Kirkpatrick 1987). Diets of grouse in the Appalachian region tend to be higher in tannin and phenol levels (potential toxins) and lower in protein levels than the diets of grouse in the northern United States and Canada (Servello and Kirkpatrick 1987). The poor nutritional quality of grouse diets in the Appalachian region may result in increased foraging time, thus increasing the risk of predation, decreased body condition, reproductive potential, and chick survival (Beckerton and Middleton 1982, Servello and Kirkpatrick 1987, Hewitt and Kirkpatrick 1996).

Few data exist on ruffed grouse productivity in the Appalachian region (Haulton 1999), but information on nesting rates, clutch sizes, hatching success, and brood survival suggest productivity is lower in the Appalachian region than in the northern United States and Canada. Bump et al. (1947) estimated $\geq 75\%$ of females attempt to nest every spring in New York, but suggested in most years all females attempt to nest. In contrast, the 2-year (1997, 1998) mean nesting rate in the Appalachian region was 81.6% (Haulton 1999). Mean clutch sizes across the northern United States and Canada average >10.5 eggs (Bump et al. 1947, Edminster 1947, Cringan 1970), compared to a mean clutch size of 9.5 eggs in the Appalachian region (Haulton 1999). Hatching success rates are similar in the Appalachian region (94%; Haulton 1999) and the northern United States and Canada (94.5%; Bump et al. 1947). Brood survival is lower in the Appalachian region than in the northern United States and Canada. Haulton (1999) reported in the Appalachians brood survivorship to 5-weeks post-hatch

was 11 – 13%, whereas Rusch and Keith (1971) reported 51% brood survival to 12-weeks post-hatch for northern populations.

Recruitment is the addition of individuals (i.e., young or immigrants) to the breeding population (Krebs 1994), and for upland gamebirds is usually indexed by the ratio of juveniles to adults in the fall harvest. Estimates of juveniles in the fall population in the northern United States and Canada ranged from 64 to 78% (Dorney 1963, Davis and Stoll 1973), compared to 49 to 53% in the Appalachian region (Davis and Stoll 1973). Average recruitment in New York was 2.5 juveniles/hen (Bump et al. 1947), and 2.0 juveniles/adult in Alberta (Gullion and Marshall 1968).

Harvest of ruffed grouse is based on several general assumptions about upland game populations (Strickland et al. 1994). These principles are 1) populations produce annual harvestable surpluses, 2) hunting seldom has adverse impacts on upland game populations, and 3) hunting pressure and harvest decreases as upland game populations decline (Strickland et al. 1994). Recent concern over the effects of late-season hunting on ruffed grouse populations (Fischer and Keith 1974, Gullion and Evans 1982) has raised a debate of these principles, but little research has directly investigated the compensatory mortality theory (Gullion 1984, Myrberget 1985, Baines and Linden 1991, Ellison 1991, Strickland et al. 1994).

Several authors have concluded sport harvest does not negatively effect ruffed grouse populations (Bump et al. 1947, Dorney and Kabat 1960, Gullion and Marshall 1968, Fischer and Keith 1974). There is evidence that harvest of <50% of rock ptarmigan (*Lagopus mutus*) (McGowan 1975), and ruffed grouse (Palmer 1956, Gromely 1996) populations is compensatory, but these studies were conducted in areas

adjacent to non-hunted areas. The non-hunted areas may have supported the ptarmigan and grouse populations on the hunted areas via immigration. Ellison (1978) concluded 57% harvest rate of male black grouse (*Tetrao tetrix*) in the French Alps was compensatory. Experimental studies on hunted and non-hunted sites in New York (Edminster 1947) and Michigan (Palmer and Bennet 1963) indicated hunting did not affect ruffed grouse populations.

Bergerud (1985) posited all grouse hunting is additive and reduces spring breeding populations. In the French Pyrenees harvest was determined to negatively effect capercaillie (*Tetrao urogallus*) population size and demographics (Baines and Linden 1991). Kubisiak (1984) concluded heavy harvest early in the season could reduce grouse numbers. In central Wisconsin, research indicated a harvest rate between 28-33% was partially, if not completely additive and on a regional basis could decrease ruffed grouse numbers (Destefano and Rusch 1986, Small et al. 1991).

The proportion of juvenile grouse in the harvest decreases as the season progresses, suggesting late-season harvest may reduce spring breeding populations (Dorney and Kabat 1960, Davis and Stoll 1973, Kubisiak 1984). Based on this conclusion, researchers have argued it is advantageous to harvest populations early in the fall to allow more time for compensatory processes to act on the population (Baines and Linden 1991). In the Appalachian region ruffed grouse hunting seasons tend to be longer than in northern United States and Canada and the majority of the harvest is suspected to occur during the late-season (late November to February, G. Norman, Virginia Department of Game and Inland Fisheries personal communication).

To successfully manage ruffed grouse populations in the Appalachian region managers must have an understanding of population trends, limiting factors, and the impact of harvest mortality. Assessing population trends, identifying limiting factors and determining the effects of hunting on ruffed grouse populations can be accomplished through manipulative, regional telemetry studies (Gullion 1984, Baines and Linden 1991). Data from such studies can be used to develop realistic and reliable population models to aid managers in developing management plans. The use of computer models has become an accepted method of evaluating proposed management plans because they can provide useful predictions of population responses to management activities and aid managers in identifying potentially unsuccessful management actions prior to field implementation (Wisdom and Mills 1999).

Our goal was to assess ruffed grouse population dynamics, identify limiting factors, and provide recommendations for ruffed grouse management in the Appalachian region. To meet our goal we established the following objectives:

1. Estimate reproductive rates and identify factors that influence reproduction,
2. Estimate survival and cause-specific mortality rates and identify factors that influence survival,
3. Determine if ruffed grouse harvest in the Appalachian region is additive or compensatory, and
4. Estimate ruffed grouse finite population growth rate in the Appalachian region and identify areas of future research needs.

STUDY AREAS

We studied ruffed grouse populations on 12 sites in 8 states throughout the Appalachian region (Table 1, Fig. 2). Land ownership varied across sites and included National Forest Land, state public land, and industrial forest land owned by MeadWestvaco Corporation. Study sites range in size from 2,000 – 11,000 ha. The proportion of forest age classes (sapling, pole, and sawtimber) varied across sites due to differences in past timber management activities. Timber management activities ranged from no active harvest to selective harvest and clearcutting. MeadWestvaco lands had the most active timber harvesting programs and thus the greatest proportion of sapling-age stands. Hunting seasons typically ran from early October to late February with daily bag limits ranging from 1 – 4 grouse and possession limits of 4 – 8.

Study sites (except OH1 and OH2) were classified as either oak-hickory (OHF) or mixed-mesophytic (MMF) forest associations based on literature review (Braun 1950), canopy tree composition and abundance data collected as part of the ACGRP (J. Tirpak, Fordham University, unpublished data), and a Relative Phenology Index (RPI) (S. Klopfer, the Conservation Management Institute, Table 1, Fig. 2). The RPI estimates the timing of phenological events and duration of growing seasons based on latitude, longitude, and elevation according to Hopkins bioclimatic rule (Hopkins 1938). We calculated RPI values for each site by based on the mean latitude, longitude, and elevation of ruffed grouse radio-telemetry locations by year (1996 – 2001) and then averaging across years. The RPI values calculated for each study site indicated that growing seasons on MM sites (i.e., higher RPI values) were shorter than on OH sites despite the interspersed of the 2 forest associations in the Appalachian region (Fig. 1).

The OH1 and OH2 study areas were not classified due to lack of canopy tree composition and abundance data.

Oak-hickory forests were dominated by chestnut oak (*Quercus prinus*), white oak (*Q. alba*), red oak (*Q. rubra*), scarlet oak (*Q. coccinea*), black oak (*Q. velutina*), shagbark hickory (*Carya ovata*), pignut hickory (*C. glabra*), mockernut hickory (*C. tomentosa*), and bitternut hickory (*C. cordiformis*). Other important tree species were red maple (*Acer rubrum*), striped maple (*A. pensylvanicum*), sugar maple (*A. saccharum*), beech, table mountain pine (*Pinus pungens*), white pine (*P. strobus*), Virginia pine (*P. virginiana*), pitch pine (*P. rigida*), and eastern hemlock (*Tsuga canadensis*). Mountain laurel and great rhododendron were important understory species. Dominant canopy species on MM sites were sugar maple, red maple, yellow birch (*Betula alleghaniensis*), basswood (*Tilia americana*), black cherry (*Prunus serotina*), pin cherry (*P. pennsylvanica*), yellow poplar (*Liriodendron tulipifera*), white pine, beech, northern red oak, and eastern hemlock. Other important species were white ash (*Fraxinus americana*), white oak, and aspen (*Populus tremuloides*). Hard mast producing species, including members of the red and white oak groups and beech were present on MM and OH forests, but were more abundant on OH sites (Fig. 3). Aspen, birch, and cherry, which provide high quality foods for grouse were more abundant on MM sites than on OH sites (Fig. 4).

METHODS

Field Methods

Appalachian Cooperative Grouse Research Project personnel (hereafter “we”) trapped ruffed grouse from August to December (fall) and February to April (spring)

between 1996 and 2002 in lily-pad traps (Gullion 1965). We assumed grouse were trapped at random and that capturing and handling did not affect grouse behavior, habitat selection, or survival. We estimated trap rate by calculating the number of grouse captured (including recaptures) per 100 trap nights of effort. We recorded the number of grouse flushed near traps during daily trap checks and estimated the flush rates by calculating the number of grouse flushed from the vicinity of traps per 100 trap nights. We recorded the mass of each bird and determined age and sex based on feather (primaries, tail, and rump) characteristics (Davis 1969, Kalla and Dimmick 1995). Each bird was classified as juvenile (hatch-year and entering first breeding season) or adult (after hatch-year). Birds were fitted with uniquely numbered aluminum leg bands and 10-g necklace-style radio transmitters with an 8-hour motion detector (Advance Telemetry Systems, Isanti, MN USA) and were released at the capture site. Released grouse had to survive a 7-day acclimation period before entering the study. Recent work in Ohio indicated radio-collars do not influence ruffed grouse survival (Swanson et al. 2003). After the 7-day acclimation period ruffed grouse were monitored ≥ 2 times per week to determine location (Whitaker 2003) and status (alive or dead).

Evaluations for 6 mast-producing plant species (red/black oak, white oak, chestnut oak, beech, grape and greenbrier) were completed between August-December of each year on each study site. We ranked mast production of each species on a scale of 0 - 3. A score of 0 indicated complete mast failure, 1 a minimal mast crop, 2 a moderate mast crop, and 3 an abundant mast crop. If a species was not present on a particular study site it was given a score of zero. We calculated an annual mast

production index for each study area [$Y = 7.96 + 6.72(\text{Chestnut Oak Score})$; Devers et al. unpublished data].

Reproductive Analysis

We monitored female ruffed grouse via radio-telemetry starting April 1 each year to determine reproductive activity. We considered birds that were triangulated in the same location over a period of several days to have initiated a nest (Vangilder and Kurzejeski 1995). To minimize disturbance to nesting birds, we flushed females from their nest only once during the 2nd or 3rd week of incubation to determine clutch size, estimate hatch date, and to record the location of the nest with a geographic positioning system. As the estimated hatch date approached, we monitored females daily for signs of movement, which indicated hatching occurred or the nest was lost. Within 1 day of the female leaving the nest we returned to the nest to determine nest fate (successful or unsuccessful) and the number of eggs successfully hatched. We estimated the number of hatched eggs by counting egg shell fragments (Vangilder and Kurzejeski 1995). Complete egg shells with piped tops were considered to have hatched. We monitored females with failed first nests ≥ 3 days per week to determine if a second nest was attempted. If a hen attempted a second nest we again flushed the hen once during the 2nd or 3rd week of incubation to determine clutch size, estimated hatch date, and to record the nest location. We continued to monitor the hen until the eggs hatched or the nest was lost, and determined the number of eggs that hatched. We estimated chick survival to 35 days post-hatch by following the radio signal of hens to the brood, flushing the brood and making ocular estimates of brood size on the 35th day post-hatch. All flush counts were conducted by ≥ 2 people. We consider this method to provide a

minimum estimate of chick survival due to the possibility of under counting chicks when the female is flushed. Thirty-five day survival was calculated as:

$$S_{35\text{-days}} = \frac{\# \text{ Chicks Counted}}{\# \text{ Chicks Hatched}} \quad (1)$$

We estimated reproductive parameters (Table 2) and used information-theoretic model selection (Burnham and Anderson 2002) to draw inferences about factors affecting ruffed grouse reproduction in the southern and central Appalachian region. Based on a literature review of ruffed grouse reproductive ecology and our experience we selected explanatory variables (Table 3) to develop *a-priori* models for each reproductive parameter. After inspection of model results, we also developed *post-hoc* models for clutch size. We compared *post-hoc* models of clutch size to the “best” *a-priori* models. Weather and temperature data used in the *a-priori* models were obtained from the National Climatic Data Center (NCDC 2003). Data were obtained for each study site by downloading data for respective counties. If a county had >1 NCDC station, data were averaged across stations.

We used logistic regression (Proc Logistic, SAS Institute 2000) to fit *a-priori* models of nest rate (NR), nest success (NS), re-nest rate (RNR), and hen success (HS). We evaluated the fit for each global model (i.e., the most highly parameterized model) using a Goodness-of-Fit Test (SAS Institute 2000). If the global model provided an adequate fit we continued with the model selection process, if the global model did not provide an adequate fit, we ended the model selection process and reported summary statistics of the variable of interest. We used several criteria to evaluate model performance including, the second order Akaike Information Criterion (AIC_c),

AIC_c differences (Δ_i), and Akaike Weights (ω_i) (Burnham and Anderson 2002). We calculated AIC_c using the -2 log likelihood obtained using the “covout” option in Proc Logistic (SAS Institute, Cary, NC). We used the quasi-likelihood adjustment (QAIC_c) if we detected over-dispersion in the data. We tested for over-dispersion (\hat{C}) in the global model based on a single variance inflation factor ($P = 0.15$) approximated with the formula (Burnham and Anderson 2002).

$$\hat{C} = \chi^2/\text{df}. \quad (2)$$

We also report concordance, discordance, and ties to facilitate model evaluation.

We used general linear mixed models (JMP, SAS Institute 1996) to evaluate the ability of our *a-priori* models to explain variation in incubation date (INCD), clutch size (Clutch), and hatchability (Hatch). We evaluated the fit of each global model by evaluating the global ANOVA test and visually inspecting residuals. We used AIC_c, Δ_i , ω_i (Burnham and Anderson 2002) to rank and evaluate models. We report R^2 , and R^2_{adj} to aid model evaluation (Eberhardt 2003). We considered models with Δ_i of ≈ 2.0 as competing models (Burnham and Anderson 2002). We tested for pair-wise correlation among continuous explanatory variables prior to fitting our *a-priori* models and removed 1 member of each pair having a correlation >0.5 . We drew conditional inferences based on single models because we were not able to calculate average beta coefficients across models due to the presence of multiple link functions in the *a-priori* model sets (David Anderson, personal communication). We report effect sizes for parameters that do not contain 0.0 in the 95% confidence interval.

Survival Analysis

Survival and cause-specific mortality data were obtained by tracking radio-collared grouse ≥ 2 times per week and recording status as alive or dead. When a mortality signal was emitted, field personnel located the carcass and determined the cause of death based on carcass remains, predatory sign in the immediate vicinity, and markings on the radio transmitter (Bumann 2002a). Cause of death was recorded as avian predation, mammalian predation, unknown predation, natural, or research-related. The date of mortality was assigned as the mid-point between the last known alive date and date mortality was discovered (Pollock et al. 1989a, 1989b). Birds that could not be located due to emigration from the study area or failed radio-transmitter were right censored (Pollock et al. 1989a, 1989b). Date of censoring was assigned 1 day after last known date alive. Data on harvested birds (date and location of harvest) were obtained via a \$25 reward inscribed on the radio-transmitter and leg band. Only birds surviving a 7-day acclimation period were included in the survival analysis.

Kaplan-Meier – We estimated site specific annual survival rates (pooled across age and sex class) using the staggered entry design (Pollock 1989a, 1989b) modification of the product limit estimator (Kaplan and Meier 1958). We used a 1-week time step starting 1 April and ending 31 March. We used a 1-week time step because all birds were monitored at least once a week in all seasons. Seasons were spring (1 April – 30 June), summer (1 July – 30 September), fall (1 October – 31 December), and winter (1 January – 31 March). Assumptions of the staggered entry design include animals are randomly sampled, individuals are independent, marking does not affect survival, censoring is independent of an animal's fate, and survival function is constant

across animals and time (Pollock et al. 1989a, 1989b). Estimates of annual survival were calculated using the known fates model in Program MARK (White and Burnham 1999) to provide estimates comparable to previous studies using similar methods. Percent of mortality due to a specific cause was calculated by dividing the number of mortalities due to each cause by the total number of mortalities during the period of interest. Cause-specific mortality rates were calculated by censoring all deaths except the cause of interest (e.g., avian predation).

Known Fates Analysis with Covariates – We used information-theoretic model selection to investigate factors influencing ruffed grouse survival using the known fates model with covariates. All analyses were conducted using Program MARK (White and Burnham 1999). We selected explanatory variables and developed *a-priori* models based on published literature and our experience. We determined the appropriate time step by fitting the global (or Full) model using a 15-day, monthly, and seasonal (spring, summer, fall, winter) time step and comparing estimates of over-dispersion (\hat{C}). We then used the time step with the lowest \hat{C} .

A limitation of model building is that it cannot accommodate missing observations, but the realities of field research often result in data sets with missing observations. To maximize our data and investigate hypotheses related to ruffed grouse survival we conducted our survival analysis on several time scales. First, we investigated survival over a 5-year period (1 April 1997 – 31 March 2002). In the trade off between duration and missing observations, this data set consisted of the fewest explanatory variables (Table 4) and *a-priori* models. Second, we analyzed survival in 5, 1-year periods (1 April – 31 March). These data sets included different combinations of

study sites depending on data completeness and additional explanatory variables including raptor abundance, alternative prey abundance, snow conditions, and temperature (Table 5) resulting in several *a-priori* models that could not be included in the full 5-year data set due to missing observations. The final analyses investigated seasonal survival patterns using a monthly time step. This analysis allowed us to maximize the use of our data and investigate factors influencing within-season survival over multiple years. We used QAIC_c, Δ_i , and ω_i to rank and evaluate models (Burnham and Anderson 2002). We used \hat{C} from the global (or full) model to correct for over-dispersion in the data. We tested for pair-wise correlation among continuous explanatory variables in the same manner as for the reproductive analyses. We did not average beta coefficients across models due to the use of multiple link functions among models (Burnham and Anderson 2002), thus we drew conditional inference based on single models. We report effect sizes for variables with point estimates and 95% confidence intervals.

Test of the Compensatory Mortality Hypothesis

To test the compensatory mortality hypothesis we conducted a manipulative field experiment on 7 study sites (Table 1). We used data from only those study areas that were active during both phases of the ACGRP. Phase I of the ACGRP was fall 1996 – summer 1999 and Phase II was fall 1999 – summer 2002. The experimental design was based on a completely randomized design with repeated measures. Four study sites (MD1, VA1, VA2, and WV1) were assigned as the control group and 3 sites (KY1, VA3, and WV2) were assigned as the treatment group. Control sites were open to hunting during each phase of the study. Treatment sites were closed to hunting during

phase II of the study. We used a repeated measures analysis of variance to test for the main effects of a treatment (open or closed to hunting) and phase (Phase 1 and Phase 2) on annual survival and reproductive effort (i.e., nesting rate, nest success, hen success, and chick survival). We also tested for interactions between treatment*phase. A significant treatment*Phase interaction would indicate that annual survival or reproduction differed, relative to phase I, between treatment and control areas after the closure of hunting on treatment areas during phase II. Due to logistic and political constraints associated with state harvest regulations and the management of public lands we were not able to randomly apply treatments to study sites, but selected the 3 study areas with the highest harvest rates between 1996 – 1998 seeking to impose the largest effect size on the experiment. All sites were open to normal state hunting regulations during phase I of the ACGRP. In Virginia the hunting season started during the last week of October and ended on the second Saturday in February. The daily bag limit was 3 birds/day. In Kentucky the hunting season started in mid-November and ended on the last day of February and the daily bag limit was 4 birds/day. The hunting season in Maryland started on the first Saturday in October and ended on 31 January. In Maryland the daily bag limit was 2 birds/day. In West Virginia the daily bag limit was 4 birds/day and the hunting season started on the second Saturday of October and continued to the end of February. Exact season dates often varied from year to year. Annual survival (1 April – 31 March) was estimated using the staggered entry design (Pollock 1989a, 1989b) modification of the product limit estimator (Kaplan and Meier 1958) as described above. Due to limited sample size, annual survival by treatment was estimated by age, sex, and pooled across age and sex classes. Cause-specific

mortality rates were estimated using the Kaplan-Meier method after censoring all mortalities due to causes other than the 1 of interest (i.e., harvest, Trent and Rongstad 1974). Percent of mortality due to a specific cause was calculated by dividing the number of mortalities due to each cause by the total number of mortalities during the period of interest.

Population Modeling

We developed deterministic and stochastic ruffed grouse population models to estimate finite population growth rate (λ), assess the influence of vital rates on λ , estimate probability of extirpation, and to evaluate hypothetical management alternatives. We modeled only the female portion of the population using a density-independent, exponential, age-structured model with a yearly time step. Each model run started with a user-defined (5,000, 10,000, 25,000, or 50,000) estimated population size, followed by estimated reproduction, recruitment, and survival. The state variable tracked over time was population size and the final output was $\bar{\lambda}$ and population viability (i.e., the proportion of model runs that ended with an extant population). We assumed a spatially closed population (i.e., no immigration or emigration) and assumed ruffed grouse longevity was 4 years, resulting in 4 age classes. Based on our reproductive and survival analyses, we assumed vital rates did not differ among age classes.

Each model was developed at 3 spatial bounds including, central and southern Appalachian regional, forest association, and study site. Each spatial scale was developed using data collected as part of the ACGRP. The regional model was developed using parameter values pooled across study sites (except OH1 and OH2

because they were not classified as either OH or MM forests) and averaged across years (Table 6). The objective of this scale was to understand regional ruffed grouse population dynamics in the Appalachians. To validate our deterministic models we compared our estimate mean λ at the regional scale to the estimate of percent population change per year in ruffed grouse abundance in the Appalachian region from the Breeding Bird Survey (Sauer et al. 2004). The objective of the forest level scale was to model the contribution of ruffed grouse populations inhabiting mixed-mesophytic forests (MMF) and oak-hickory forests (OHF) to regional population dynamics. The MMF model was developed using parameter estimates pooled across study sites classified as MM forests and averaged across years (Table 6). Parameters for the OHF were estimated by pooling data across study areas identified as dominated by oak-hickory forest association and averaged across years. The mixed-mesophytic study area (MMS) model was developed using parameter estimates averaged across study areas classified as mixed-mesophytic and years. The oak-hickory study area (OHS) model was developed in the same manner using data from oak-hickory dominated study areas. The objective of this site-level scale was to increase our understanding of local population dynamics at a spatial scale typical of most state wildlife management areas. We were unable to validate our estimates of λ at the forest or study site scale due to a the lack of similar spatial scale estimates in the Breeding Bird Survey.

Each time step started on 1 April with reproduction by adult birds (ages 1 -4), followed by recruitment, and finally survival of adult birds, resulting in estimated abundance of birds ages 1-4. Juvenile birds were assumed to graduate to adults on 1 April of the year after hatch.

Deterministic Models

Modeling Approach - We initially developed 2 alternative modified Leslie matrix (Wisdom and Mills 1997) deterministic models to estimate stable age distribution, mean fecundity, and λ at each spatial scale. We also conducted elasticity analyses to assess the influence of vital rates on λ .

Model 1 - The first model (hereafter model 1, Fig. 5) estimated mean fecundity (F), defined as the number of female offspring produced in a unit time (Krebs 1994) and used it at each time step. We estimated F as function of multiple secondary vital rates (Table 7) using the formula:

$$F = \{[(N * E * G * C * H) + (((N - (N * E * G)) * I) * J * K * L)] * B\} * X \quad (3)$$

Where:

N = number of hens (ages 1 – 4) on 1 April

E = mean nesting rate

G = mean nest success rate

C = mean clutch size

H = mean hatchability

I = mean re-nest rate

J = mean nest success rate for second nests

K = mean clutch size for second nests

L = mean hatchability for second nests

B = mean 35-day chick survival rate as a function of mean mast

Production (M; Table 7)

X = constant (0.5) assuming a 1:1 sex ratio at hatch

We assumed secondary vital rates were not correlated with each other. Recruitment (R) is defined as the increment to a natural population, usually from juvenile animals entering the breeding population (Krebs 1994) and was calculated using the formula:

$$R = F * S_f * S_w \quad (4)$$

Where:

F = fecundity

S_f = fall survival rate

S_w = winter survival rate

Female population size was calculated using the following equation:

$$N_{t+1} = N_t * S' + R \quad (5)$$

Where:

N = number of adult female ruffed grouse (ages 1 – 4).

t = year.

S' = annual adult survival rate

$$S' = S_p * S_s * S_f * S_w \quad (6)$$

Where:

S_p = spring survival rate

S_s = summer survival rate

S_f = fall survival rate

S_w = winter survival rate

t = year

Finite growth rate (λ) was calculated using the formula:

$$\lambda = N_{t+1}/N_t$$

Deterministic model 2 (hereafter model 2, Fig. 6) was structurally the same as model 1. Recruitment and survival were estimated in the same manner, but fecundity was estimated using 1 parameter. Fecundity (F') was defined as the number of chicks alive at 35 days post-hatch per adult female alive on 1 April. By consolidating fecundity into 1 parameter we were able to incorporate correlation among secondary vital rates (i.e., nest rate and nest success) and potentially decrease measurement error. As in model 1, fecundity was modeled as a function of mean mast production (Table 7).

Estimation of Stable Age Distribution – Using the deterministic models we estimated stable age distributions for each spatial scale by entering an initial population size (N_0) of 100,000 with equal age distributions (25,000 individuals in each age class 1 – 4) and projecting population size 10 – 20 years into the future. The proportion of the population in each age class was calculated at each time step until a stable age distribution was obtained. The estimated stable age distribution was then used for all subsequent model runs.

Elasticity analyses – We performed elasticity analyses to investigate the influence of each demographic parameter on λ . First, we estimated mean λ using mean values for each demographic variable. Next, we increased the value of 1 demographic parameter (holding all others constant) from 10 – 90% of the mean value in increments of 10 and calculated λ . We repeated this process for each demographic parameter in the model and determined which parameters had the greatest influence on λ .

Stochastic models

We next developed a stochastic model to investigate variation in population growth rate over time and population viability. Based on the results from our

deterministic models (i.e., estimates of λ and fecundity) we decided to develop a stochastic version of only model 2. Fecundity (F') was again measured as the number of female chicks alive at 35-days post-hatch per female alive on 1 April (Table 7).

Recruitment was estimated using the following equation:

$$R_t = F'_t * S_{f,t} * S_{w,t} \quad (7)$$

Where:

F' = fecundity at time t

$S_{f,t}$ = fall survival rate at time t

$S_{w,t}$ = winter survival rate at time t

Population growth was modeled using the following equation:

$$N_{t+1} = N_t * S'_t + R_t \quad (8)$$

Where:

N = number of adult female ruffed grouse.

t = year.

S' = the annual adult survival rate (calculated in objective 1)

$$S' = S_{p,t} * S_{s,t} * S_{f,t} * S_{w,t} \quad (9)$$

$S_{p,t}$ = spring survival at time t drawn from a normal distribution

$S_{s,t}$ = summer survival at time t drawn from a normal distribution

$S_{f,t}$ = fall survival at time t drawn from a normal distribution

$S_{w,t}$ = winter survival at time t drawn from a normal distribution

Modeling procedure: Reliable estimates of ruffed grouse abundance at each spatial scale (i.e., regional, forest, study site) are lacking. Due to this lack of information we conducted multiple model runs with multiple initial population sizes (1,000, 5,000,

10,000, 25,000, and 50,000) and projected population size into the future over 20 and 100 year periods. Each scenario included 1,000 simulations. Two state variables were recorded during each simulation, mean finite population growth rate and population status. Mean finite growth was estimated by averaging annual growth rates over the projected time period during each simulation. Population status at the end of the projected time period was recorded as either extant or extinct. The mean annual finite growth rate was averaged across the 1,000 simulations, and population viability defined as the proportion of the 1,000 simulations that ended with an extant population.

Evaluation of hypothetical management – We investigated the potential to increase λ by increasing mean annual mast production via timber management. Research conducted on hard mast production has indicated annual production can be increased by 133% through a variety of silvicultural practices (Healy 1997). We model 4 hypothetical management activities that increased mean annual hard mast production by 50%, 75%, 100%, and 125%. We assessed these management alternatives using model 4. The initial population size was set at 25,000 and the projected time frame was 100 years. Again, we ran 1,000 simulations with each model.

RESULTS

We captured 3,118 ruffed grouse between fall 1996 and spring 2002, including 413 recaptures. The mean trap rate (pooled across sites and years) was 2.37 grouse/100 trap nights (± 0.263 s.e., 95% C.I. = 1.84 – 2.90 grouse/100 trap nights; Table 8). Mean trap flush rate (during the course of checking traps; pooled across sites and years) was 1.37 flush/100 trap nights (± 0.149 s.e., 95% C.I. = 1.07 -1.67 flushes/100 trap nights, Table 8). The mean juvenile:adult female ratio was 0.56

(± 0.080 s.e., 95% C.I. = 0.40 – 0.72, Table 9) and the mean juvenile female:adult female ratio was 0.28 (± 0.046 , s.e., 95% C.I. = 0.19 – 0.37, Table 9). Site specific reproductive and survival rates are reported in Appendix A. Forest specific reproductive and survival rates are reported in Appendix B.

Reproductive Analysis

We monitored 467 hens during nest and brood seasons between 1997 – 2002, and estimated mean nest rate, nest initiation date, clutch size, re-nest rate, nest success, hen success, and chick survival (Table 10).

Nesting rate - - The overall nesting rate was 0.96 (Table 10). The final data set used to model nesting rate consisted of 279 records from spring 1997 to spring 2002. This final data set did not include records from OH1, OH2, or NC1 due to the absence of mast evaluation data. The global model provided an acceptable fit (Goodness of Fit test $\chi^2 = 1.086$, 4 df, $P = 0.897$, $\hat{c} = 0.275$). The best model (model 18, Table 11) indicated nesting rate was a function of differences in forest associations and yearly stochasticity. Model 19 was 6.4 times more likely to be the best model than the next competing model. Mean nesting rate was higher on MM forests ($\bar{x} = 1.0$, 0.0 s.e., $n = 147$) than on OH forests ($\bar{x} = 0.86$, 0.030 s.e., 95% CI = 0.80-0.92, $n = 132$); nesting rate ranged from 0.71-1.0 across years on OH forests. The remaining models did not receive support as competing models (Table 11).

Incubation Date – The mean date of incubation initiation for 351 nests was 1 May (Table 10). The INCD data set for modeling contained 176 observations. The global model provided adequate fit ($F_{23,152} = 4.98$, $P < 0.0001$) and the residuals were normally distributed. Model 10 received the greatest support and was 5.4 times more likely to be

the best model than the next competing model (Table 12). Mean incubation date ranged from 27 April to 8 May across study areas. Adult hens initiated incubation 3.6 days (± 0.882 s.e., 95% C.I. = 1.8 – 5.3 days) earlier than juvenile hens. Remaining parameters (Mast, $DPNT_{(win)}$, and $MMNT_{(win)}$) had confidence intervals for the β_i 's that included 0.0.

Clutch Size – The mean clutch size was 9.86 (Table 10). The clutch size data set included 211 observations (Table 13). The global model provided an adequate fit ($F_{28,182} = 2.35$, $P = 0.0004$) and the residuals were normally distributed. There was little support for any of our *a-priori* models (Table 13), thus we developed several post-hoc models to gain more insight into variation in clutch size (Table 14). Our final post-hoc clutch size data set consisted of 186 observations. The global model fit was acceptable ($F_{14,171} = 1.96$, $P = 0.024$). Post-hoc model selection supported 3 posteriori models over the 2 most-supported *a-priori* models (Table 14). Model E received the greatest support (Table 14) and was 4.8 times more likely to be the best model than the next competing model. Model E indicated variation in clutch size was a function of differences in forest association, study areas nested within forest associations, and incubation date. Mean clutch size was larger on MM forests than on OH forests by 0.97 eggs (± 0.238 s.e., 95% CI = 0.49 – 1.45 eggs). Mean clutch size ranged from 9.6 – 11.2 eggs across study sites. Mean clutch size was negatively related to nest initiation date ($\beta = -0.071 \pm 0.022$, 95% C.I. = -0.114 - -0.029).

Hatchability – The complete data set for hatchability included 384 nests. Median hatchability for 384 nests was 0.82 (Table 10). The hatchability data set used in the

model selection procedure contained 144 observations. However, model selection was not used due to the poor fit of the global model ($F_{17,126} = 0.8126$, $P=0.676$).

Nest Success – The overall nest success was 0.66 for 410 nests. Our NS data set for modeling consisted of 226 records. The global model provided adequate fit (Goodness-of-Fit $\chi^2 = 5.6040$, $P = 0.5867$, $\hat{c} = 0.801$). Several models received support in explaining variation in nest success, but no single model was clearly better than the others (Table 15). The most supported model (model 16) indicated variation in nest success was a function of mast production ($\beta_{\text{logit}} = -0.507 \pm 0.231$ s.e., 95% CI = $-0.959 - -0.055$), MMNT(Mar & Apr) ($\beta_{\text{logit}} = -0.196 \pm 0.0898$ s.e., 95% CI = $-0.372 - -0.02$), and an interaction between mast*MMNT(Mar & Apr) ($\beta_{\text{logit}} = 0.016 \pm 0.007$ s.e., 95% CI = $0.002 - 0.029$). Models 1 and 8 received limited support (Table 15) and indicated mean nest success varied across study areas (0.53 – 0.94) and years. Mean nest success was higher, but not different in MM forests ($\bar{x} = 0.70$, ± 0.040 s.e., 95% CI = 0.62-0.78, $n=131$) than on OH forests ($\bar{x} = 0.63$, ± 0.050 s.e., 95% CI = 0.53-0.73, $n=95$).

Re-nest rate – The overall re-nest rate was 0.23 (Table 10). Our RNR data set consisted of 64 records from MD1, PA1, VA1, VA2, WV1, and WV2. The global model provided an adequate fit ($\chi^2 = 10.18$, $P = 0.258$). We used QAIC_c to evaluate and rank models because there was evidence of over-dispersion ($\hat{c} = 1.27$) in the data. Three models were considered to be competing models (Table 16). Model 23 received the greatest support and was 1.37 times more likely to be the best model than model 6 and 4.01 times more likely than model 9. Model 23 indicated re-nest rate was a function of differences in forest associations. Mean re-nesting rate was higher on MM forests ($\bar{x} = 0.45 \pm 0.088$ s.e., 95% C.I. = 0.28 – 0.62) than on OH forests ($\bar{x} = 0.03 \pm 0.032$ s.e.,

95% C.I. = 0.00 – 0.10). Model 6 indicated re-nest rate was negatively correlated with $MMNT_{(win)}$ ($\beta_{logit} = -0.188 \pm 0.095$ s.e., 95% CI = -0.375 - -0.002). Similar to Model 23, Model 9 suggested re-nest rate was a function of differences in forest associations and mast production the previous fall. Estimated beta value and confidence interval for mast included 0.0.

Hen success – Overall mean hen success for 412 hens was 0.68 (Table 10). The HS data set consisted of 230 observations. The global model provided adequate fit ($\chi^2 = 0.0002$, $P = 1.0$, $\hat{c} = 0.0$). Several models received similar support for explaining variation in hen success (Table 17). The 3 competing models indicated variation in hen success was a function of differences in forest association, mast production, and an interaction between forest association and mast production. Estimates based on model 28 indicated hen success was higher, but not different on MM forests ($\bar{x} = 0.70$, 95% C.I. = 0.4– 0.92, $n = 133$) than OH forests ($\bar{x} = 0.63$, 95% C.I. = 0.56 0.83, $n = 99$). Beta estimates and confidence intervals for mast and interaction terms overlapped 0.0.

Chick Survival -- Our 35-day chick survival data set for modeling included 145 observations, and overall chick survival for 235 broods was 0.22 (Table 10). The residuals of the global model were normally distributed and the fit was acceptable ($F_{16,128} = 2.002$, $P = 0.0174$, $R^2 = 0.11$, Table 18) Model 4 was the best model and was 3.44 times more likely to be the best model than the next most supported model but the explanatory power was extremely low ($R^2 = 0.04$; Table 18). Model 4 indicated chick survival to 35-days post-hatch was positively related to mast production ($\beta = 0.003 \pm 0.001$ s.e., 95% C.I. = 0.00 – 0.005, Fig.7). Mean 35-day chick survival (pooled across study areas and years) was 0.21 (± 0.019 s.e., 95% C.I. = 0.18 – 0.25, $n = 145$).

Survival Analysis

Kaplan-Meier – Mean annual survival of ruffed grouse (averaged across sites and years) in the Appalachian region was 0.42 (± 0.022 s.e., 95% C.I. = 0.38 – 0.46) and ranged from 0.17 to 0.57 across study areas (Table 19). Avian predation was the leading cause of known mortalities, followed by mammalian predation (Fig. 8). Estimates of cause-specific mortality rates produced similar results. Avian predation rate was higher ($\bar{x} = 0.32 \pm 0.020$, 95% C.I. = 0.28 – 0.36) than other cause-specific mortality rates including mammalian predation rate ($\bar{x} = 0.21 \pm 0.018$, 95% C.I. = 0.17 – 0.24), and predation rate by unidentified predators ($\bar{x} = 0.13 \pm 0.025$, 95% C.I. = 0.08 – 0.18). The mean natural mortality rate was 0.54 (± 0.023 , 95% C.I. = 0.50 – 0.59). The mean harvest rate across sites and years was 0.10 (± 0.014 s.e., 95% C.I. = 0.07 – 0.13) excluding treatment sites between 1999 and 2002.

Survival 1997 - 2002 – Ruffed grouse survival from April 1997 – March 2002 was modeled in Program MARK using data from MD1, VA2, VA3, WV1, and WV2 with records for 1,064 individual ruffed grouse. Fit of the global model (i.e., full model) was assessed by evaluating \hat{c} and inspecting residuals. There was evidence of over-dispersion in the data ($\hat{c} = 3.14$), but residuals were normally distributed. The best model (5, Table 20) indicated survival was a function of differences between OH and MM forest associations and seasonal variation. Survival was higher on OH forests than on MM forests ($\bar{x} = 0.03$, 95% C.I. = 0.01 – 0.06), and was highest in summer and lowest in winter (Fig. 9). This model was 1.6 times more likely to be the best model than the next competing model (Table 20).

Model 14 received moderate support ($\omega_{14} = 0.30$) and indicated ruffed grouse survival during this period was a function of differences in forest associations, age, and season. Survival was higher on OH forests than on MM forests ($\bar{x} = 0.02$, 95% C.I. = 0.01 – 0.04). Seasonal survival was highest in summer and lowest in winter. Although age was included in the model, the 95% confidence interval overlapped 0.0.

Survival 1997 - 1998 – Our data set for April 1997 – March 1998 survival analysis consisted of 273 individual grouse from MD1, VA2, VA3, WV1, and WV2. The global model provided adequate fit ($\hat{c} = 2.45$) and the residuals were normally distributed. Our best model (model 2, Table 21) indicated survival varied by season. Survival was highest in summer ($\bar{x} = 0.94$, 95% C.I. = 0.89 – 0.97), followed by spring ($\bar{x} = 0.82$, 95% C.I. = 0.75 – 0.88), fall ($\bar{x} = 0.79$, 95% C.I. = 0.72 – 0.83), and winter ($\bar{x} = 0.72$, 95% C.I. = 0.63 – 0.79). The model weight indicated model 2 had a 58% probability of being the best model and that it was 4.2 times more likely to be the best model than the next competing model.

Survival 1998 - 1999 – The data set for 1998 – 1999 survival consisted of 328 individuals from MD1, VA1, VA2, VA3, WV1, and WV2. The global model had an estimated $\hat{c} = 2.068$ and the residuals were normally distributed. Model 2 had the greatest support ($\omega_i = 0.24$, Table 22) and indicated survival was a function of seasonal variation. Survival was highest in summer ($\bar{x} = 0.94$, 95% C.I. = 0.90 – 0.97), followed by winter ($\bar{x} = 0.84$, 95% C.I. = 0.77 – 0.89), fall ($\bar{x} = 0.83$, 95% C.I. = 0.77 – 0.88), and spring ($\bar{x} = 0.76$, 95% C.I. = 0.68 – 0.82). Annual survival was 0.50 (95% C.I. = 0.36 – 0.62).

Model 8 received only slightly less support ($\omega_i = 0.23$), but confidence intervals on the difference for each sex and age class overlapped 0. Survival was highest in summer ($\bar{x} = 0.94$, 95% C.I. = 0.93 – 0.95), followed by winter ($\bar{x} = 0.81$, 95% C.I. = 0.80 – 0.83), fall ($\bar{x} = 0.81$, 95% C.I. = 0.80 – 0.83), and spring ($\bar{x} = 0.75$, 95% C.I. = 0.73 – 0.77) in this model.

Model 14 also received moderate support and indicated survival was a function of forest association, age, sex, age*sex, MMNT(win), and SNOW (Table 22). Ruffed grouse in MM forests had slightly higher survival ($\bar{x} = 0.01$, 95% C.I. = 0.0 – 0.02) than grouse in OH forests, but the difference was not significant. Survival was negatively related to SNOW ($\beta_{\text{logit}} = -0.164 \pm 0.063$ s.e., 95% CI = -0.295 - -0.04). Remaining explanatory factors in the model had confidence intervals that overlapped 0.

Survival 1999 - 2000 – The 1999 – 2000 survival data set consisted of 396 records and included data from MD1, PA1, VA1, VA2, VA3, WV1, and WV2. The global model provided a good fit ($\hat{c} = 2.06$) with normally distributed residuals. Model 12 received the greatest support (Table 23) and was twice as likely to be the best model as the next competing model. Inference based on Model 12 indicated ruffed grouse survival was higher in OH forests ($\bar{x} = 0.07$, 95% C.I. = 0.05 – 0.10) than in MM Forests (Table 24). Adult survival was slightly higher ($\bar{x} = 0.02$, 95% C.I. = 0.00 – 0.04) but not different from juvenile survival. Survival was positively related to raptor abundance ($\beta_{\text{Raptor}} = 0.24$, 95% C.I. = 0.07 – 0.41). Confidence intervals for the remaining parameters included 0.0.

Model 14 received moderate support (Table 23) and indicated survival was a function of forest association, age, sex, age*sex, SNOW, MMTN(win), and

SNOW*MMTN(Win). This model indicated ruffed grouse survival was higher in OH forests by 0.09 (95% C.I. = 0.06 – 0.13) than in MM Forests. Again, adult ruffed grouse survival was slightly higher ($\bar{x} = 0.02$, 95% C.I. = 0.00 – 0.04), but not significantly different than juvenile survival. Survival was negatively related to MMNT(win) ($\beta_{\text{MMNT(win)}} = -0.26$, 95% C.I. = -0.44 – -0.08). The remaining beta coefficients had confidence intervals that included 0.0.

Model 6 also received moderate support (Table 23) and indicated survival was a function of differences in forest association and seasonal variation (Table 24). Survival was highest in summer and lowest in fall.

Average across the 3 competing models (Models 12, 14, and 6) mean summer survival was 0.93 (± 0.003 se), mean spring survival was 0.85 (± 0.012 se), mean winter survival was 0.84 (± 0.006 se), and mean fall survival was 0.81 (± 0.007 se).

Survival 2000 - 2001– The 2000 – 2001 survival data set included 327 records including data from MD1, PA1, VA1, WV1, and WV2. The global model had normally distributed residuals and good fit ($\hat{c} = 1.94$). Our best model for estimating survival included differences between forest association, mast production, and an interaction between forest association and mast production (Table 25). This model was 4.3 times more likely to be the best model than the next competing model. Ruffed grouse in OH forests had higher survival than grouse in MM forests (Table 26). Seasonal survival was highest in summer and lowest in spring on OH and MM forests. Parameter estimates for the influence of mast production during each season included 0.0.

Survival 2001 – 2002 – The final data 2001-2002 data set consisted of 219 records from KY1, PA1, VA2, and WV2. The estimate of over-dispersion for the global

model was 2.025 and the residuals were normally distributed. Our best model indicated survival varied by season (Table 27). Survival was highest in the summer ($\bar{x} = 0.93$, 95% C.I. = 0.85 – 0.97), followed by spring ($\bar{x} = 0.92$, 95% C.I. = 0.83 – 0.96), winter ($\bar{x} = 0.83$, 95% C.I. = 0.72 – 0.90), and fall ($\bar{x} = 0.74$, 95% C.I. = 0.64 – 0.81). Annual survival was 0.53 (95% C.I. = 0.33 – 0.68). This model had a 39% probability of being the best model, but was only 1.22 times more likely to be the best model than the next competing model (Table 27).

Model 6 received moderate support (Table 27) and indicated survival between April 2001 and March 2002 was a function of forest association and seasonal variation. Ruffed grouse seasonal survival was higher in OH forests ($\bar{x} = 0.04$, 95% C.I. = 0.02 – 0.05) than in MM forests.

Fall Survival – The final fall survival data set included 1,006 records and included data from KY1, MD1, PA1, RI1, VA1, VA2, VA3, WV1, and WV2. The global model provided adequate fit with normal residuals and $\hat{c} = 1.35$. The best model (Model 14, Table 28) had a 60% probability of being the best model. Model 14 was 3.37 times more likely to be the best model than the next competing model. Model 14 indicated fall survival was a function of study area, year, time (i.e., month), and age. Adult grouse had higher survival ($\bar{x} = 0.02$, 95% C.I. = 0.01 – 0.03) than juveniles in the fall. Remaining explanatory factors in this model had 95% confidence intervals that overlapped 0.0.

Winter Survival – The winter survival data set consisted of 876 records including data from KY1, MD1, PA1, RI1, VA1, VA2, VA3, WV1, and WV2. The global model provided an adequate fit ($\hat{c} = 1.37$) and the residuals were normally distributed. Several

models received moderate support as the best model (Table 29). Model 5 received the most support, but was only 1.58 times more likely to be the best model than the next competing model. Model 5 indicated winter survival was a function of age, year, and month. Survival was highest in February ($\beta_{\text{logit}} = 0.18$, 95% C.I. = 0.05 – 0.31). The confidence interval of the estimated effect size of age overlapped 0.0, indicating a weak or non-existing effect on survival.

Model 9 provided similar results as model 5 and indicated winter survival was a function of age, sex, age*sex, year, and month. Point estimates and confidence intervals for each year and time indicated survival varied across years and months. Adults had higher winter survival than juveniles ($\beta_{\text{cloglog}} = 0.04$, ± 0.014 , 95% C.I. = 0.01 – 0.07). Confidence intervals of the beta estimates for the influence of sex and the presence of an interaction included 0.0.

Spring Survival – The final spring survival data set consisted of 841 records, including records from KY1, MD1, PA1, RI1, VA1, VA2, VA3, WV1, and WV2. The estimate of over dispersion was low ($\hat{c} = 1.35$) and the residuals were normally distributed. Model 6 received the greatest support (Table 30), but was only 1.17 times more likely to be the best model than the next competing model. Model 6 indicated spring survival was a function of sex, year and month. Males had higher survival than females (Table 31).

Model 18 received moderate support as a competing model (Table 30) and suggested spring survival was a function of age, sex, year, and time. Males had higher survival than females (Table 32). Survival varied by year, but not by month.

Model 10 received limited support as the best model (Table 30) and provided similar results to model 18. Survival was higher for males than females (Table 33) and varied among years. Across the 3 competing models mean survival of females in spring was 0.81 and mean survival of males in spring was 0.85.

Summer Survival – The final summer survival data set consisted of 1,176 records from KY1, MD1, PA1, RI1, VA1, VA2, VA3, WV1, and WV2. The global model provided an adequate fit ($\hat{c} = 0.60$). Only 2 models (7 and 8) were supported as competing models (Table 34). Our best model (model 7) indicated survival was influenced by forest, year, and month (Table 35). This model was 2.62 times more likely to be the best model than the next competing model. The only other competing model (model 8) indicated summer survival was a function of forest, sex, year, and time (Table 36). Again, this model indicated survival varied by year and month, but the confidence interval for sex overlapped 0. Averaged across the 2 competing models mean survival in July was 0.96 (± 0.0 s.e.), 0.98 (± 0.0 s.e.) in August, and 0.96 (± 0.0 s.e.) in September.

Test of the Compensatory Mortality Hypothesis

Hunters harvested 117 radio-collared birds (including legal harvest, crippling loss, and illegal harvest) between fall 1996 and fall 2001. Hunters harvested birds during each month of the hunting season (Table 37) and 1 bird was illegally harvested in March. Annual survival (pooled across sex and age classes) did not differ between control and treatment groups, by phase, year (nested in phase), nor was there evidence of an interaction between treatment and phase or treatment and year (nested with phase) (Table 38, Fig. 10). Comparison of annual survival rates across treatment study

areas indicated variable responses to the closure of hunting (Fig. 11). There was no evidence of a treatment*year (nested within phase) interaction for adult annual survival ($F_{3,18.6} = 1.37$, $P = 0.2821$), juvenile annual survival ($F_{3,18.2} = 0.76$, $P = 0.531$), male annual survival ($F_{3,18.7} = 0.13$, $P = 0.938$), or female annual survival ($F_{3,17.9} = 0.29$, $P = 0.831$). Further we found no evidence of a treatment*phase interactions for nest rate ($F_{1,24} = 0.07$, $P = 0.797$), nest success ($F_{1,21.5} = 1.97$, $P = 0.175$), hatchability ($F_{1,21.5} = 1.16$, $P = 0.294$), or chick survival to 35-days post-hatch ($F_{1,22.9} = 2.63$, $P = 0.119$).

The mean harvest rate on control sites between 1996 and 2001 was 0.08 (± 0.0017 se, 95% CI = 0.05 – 0.12). The mean harvest rate on treatment sites between 1996 – 1999 was 0.20 (± 0.0 se). There was evidence of a treatment*phase interaction ($F_{1,18.6} = 11.12$, $P = 0.004$) indicating harvest rates changed after the closure of hunting on the 3 treatment sites (Fig. 12). Estimates of harvest rates included illegal harvest and thus did not equal 0 in all years on the treatment sites.

Population Modeling

Deterministic Models - The objective of our deterministic modeling procedure was to estimate λ , fecundity (F and F' for models 1 and 2 respectively) and to assess the influence of vital rates on population growth. Stable age distributions were fairly constant across spatial scales (Table 39) and were used in all deterministic and stochastic model runs. Estimates of λ and fecundity differed greatly between the 2 deterministic models and were higher at each spatial scale for model 2 than model 1 (Table 40). The estimated mean λ from model 1 (0.78) was much lower than the trend in ruffed grouse abundance in the Appalachian region (-5% change/year) based on the breeding bird survey (Sauer et al. 2004). However, our estimate of mean λ (0.95) at the

regional scale based on model 2 indicates a similar trend as the breeding bird survey (Sauer et al. 2004).

Elasticity analyses indicated chick survival (model 1; Fig. 13) and fecundity (model 2; Fig. 14) had the greatest influence on λ . Winter and fall survival had relatively moderate influence on λ in each model (Fig. 13 & 14). The influence of chick survival as a function of mast production the previous fall (i.e., the influence of mast, model 1; Fig. 13) and the influence of mast production on fecundity (i.e., model 2; Fig. 14) had less influence on λ .

Stochastic models – Estimates of λ based on our stochastic model were similar to estimates based on model 2 and varied across spatial scales (Table 41). Our Estimates of λ never exceeded 1.0 at either the regional or MMF scales (Fig. 15). In contrast 18% of model runs at the MMS scale indicated positive population growth (Fig. 15). Additionally, 100% of model runs at the OHF and OHS scales resulted in estimates of mean λ of >1.0 (Fig. 15). Variation of finite population growth rate was greatest at the MMS scale and appeared to the least at the regional scale (Fig. 15). Estimates of population viability at the regional, MMF, and MMS spatial scales were extremely low, but were high for OHF and OHS spatial scales (Table 42). Results from our stochastic model indicated λ could be increased by 0.005 - 0.02 at all spatial scales by increasing mean mast production by 50% - 125% (Fig. 16).

DISCUSSION

Reproductive Analysis

Nesting rate – Ruffed grouse nesting rate differed between major forest associations in the Appalachian region, with 100% of females in MM forests and only

86% of females in OH forests nesting in a given year. Our estimates of nesting rate in MM forests were similar to rates reported in the core of the species range, but lower in OH forests. It is possible that we did not detect some nests on OH forests before they were destroyed, but due to our intensive monitoring efforts and success of documenting high nesting rate on MM forests we are confident some females in OH forests did not nest in some years. Bergerud (1988) concluded most females of all forest grouse species attempt to nest each year. During the course of their study, Gardner Bump and his co-workers in New York reported 100% nesting rate during 7 of 10 years, but estimated nesting rate may have been as low as 75% in some years (Bump et al. 1947); they concluded non-nesting was a minor factor in ruffed grouse productivity. Similarly, Larson (1998) using radio-telemetry methods similar to ours, estimated nesting rate in Michigan was 65%, but argued all females probably attempted to nest. Several researchers working throughout Wisconsin reported 100% nesting rate (Holzwardt 1990, Balzer 1995, Small et al. 1996).

Our estimate of low nesting rate in OH forests suggest habitat quality may be lower than in MM forests and northern hardwood forests. Bump et al. (1947) suggested non-nesting females may be “physiologically upset and unable to breed properly.” Though they did not elaborate on the mechanism(s) involved, others have suggested that ruffed grouse in the Appalachians may be nutritionally stressed and enter the reproductive season in poor body condition (e.g., with lower lipid and protein reserves) resulting in lower reproductive effort and success (Norman and Kirkpatrick 1984, Servello and Kirkpatrick 1987, Hewitt and Kirkpatrick 1996). The influence of female condition on avian reproduction has been demonstrated in many species (Nager et al.

2000, Reynolds et al. 2003, Verbove et al. 2003). For example, Jones and Ward (1976) concluded the proximate control of breeding in red-billed queleas (*Quelea quelea*) was female body condition, specifically protein reserves. Ruffed grouse diet in the Appalachian region has been shown to be lower in metabolizable energy and crude protein, and higher in total phenols and tannins (Norman and Kirkpatrick 1984, Servello and Kirkpatrick 1987) than in core areas. Though the authors did not directly identify their study areas as oak-hickory forest associations, each of these studies were conducted in western Virginia in areas dominated by oak and hickory. Further, ruffed grouse in the Appalachians have been shown to rely heavily on hard mast production, including acorns of red/black and white oaks and beech nuts (Norman and Kirkpatrick 1984, Servello and Kirkpatrick 1989), but hard mast production is highly variable from year to year (Healy 1997). In years of poor hard mast production, the most available foods during winter are low quality, potentially toxic leaves and twigs of evergreen species such as mountain laurel. Ruffed grouse experiencing these conditions enter the breeding season in poor condition (Long et al. 2004a) and may not have the reserves to nest. Observations on the VA1 study area support this contention. Following an extremely poor mast production year in the fall of 1997, none of 6 radio-collared females attempted to nest in the spring of 1998.

Incubation date – Ruffed grouse incubation date in the Appalachian region varied by female age and across study areas. On average, adult females started incubation 3.5 days earlier than juvenile females (i.e., first time breeders). Earlier incubation in adults is common among tetraonid species. Adult ruffed grouse in Minnesota initiated incubation approximately 2 days earlier than juveniles (Maxon 1978), similar to our

estimated difference of 3.5 days. Adult black grouse (*Tetrao tetrix*) in the French Alps initiated incubation several days earlier than juveniles (Caizegues and Ellison 2000). Begerud (1988) hypothesized that grouse should initiate nesting as early as possible (without increasing the risk of nest predation) to provide an opportunity to re-nest (if necessary) and to ensure chicks are hatched when food is abundant and weather is mild. Adult ruffed grouse may be able to initiate egg-laying and incubation earlier than juveniles because they are more familiar with their home range and have greater experience in searching for nest sites and establishing nests.

Initiation of reproductive activities of avian species in the northern hemisphere is strongly correlated with latitude and generally follows the onset of phenological events (e.g., spring green up) northward (Welty and Baptista 1988). Our results indicated incubation date varied by study area and tended to be earlier on southern study areas than on more northern study areas. Mean incubation date was earliest on VA2 (15 April), followed by VA1 (17 April), WV2 (20 April), WV1 (21 April), MD1 (22 April) and PA1 (28 April). Previous studies often have reported mean hatching dates, but we feel our analysis of incubation date can be compared to previous studies because ruffed grouse have a relatively constant rate of egg-laying and incubation period (~24 days; Bump et. al 1947), therefore incubation and hatching dates are strongly correlated. Ruffed grouse peak hatching dates show a general latitudinal trend, with peak hatching occurring earlier in the southern edge of its range and later in the central and northern portion. Peak hatching occurred during the last week of May in northeastern Iowa (Porath and Vohs 1972), the last week of May and first week of June in New York (Bump et al. 1947), Wisconsin (Hale and Wendt 1951, Maxon 1978) and Ontario

(Cringan 1970), and between the first and third week of June in Minnesota (Kupa 1966). We believe our results and those of previous studies on hatching dates indicate the proximate factor cuing the initiation of reproductive activities in ruffed grouse are increasing day-length and associated timing of phenological events (Bump et al. 1947).

Clutch size – Ruffed grouse clutch size (of first nests) in the Appalachian region was a function of study area (nested within forest association), forest association, and incubation date. Similar to the initiation of reproductive activities, clutch size in many bird species increases with increased latitude (Lack 1968, Welty and Baptista 1988). This general relationship is believed to be due to latitudinal differences in seasonal food availability, mortality rates, day length, and length of the breeding season (Welty and Baptista 1988). Our results support this generalization as mean clutch size by study area tended to increase with latitude. The VA2 study area had the smallest mean clutch size (9.22 eggs) followed by VA1 (9.45 eggs), WV2 (9.53 eggs), WV1 (10.48 eggs), PA1 (10.18 eggs) and MD1 (11.34 eggs).

Mean clutch size in MM forests (10.37 eggs) was 0.97 eggs larger than mean clutch size on OH forests (9.40 eggs). Our estimate of mean clutch size in OH forests is much lower than previously reported in the core of the species range, whereas, mean clutch size in MM forests is slightly lower, but within the range of previously reported estimates. Estimates of ruffed grouse mean clutch size (from first nest attempts) in the Great Lakes and southern Canada region range from 10.0 – 12.2 eggs (Bump et al. 1947, Edminster 1947, Marshall and Gullion 1965, Cringan 1970, Rusch and Keith 1971, Maxon 1978). Only Kupa (1966) studying ruffed grouse in Minnesota reported a mean clutch size (9.9 eggs) similar to our estimate of 9.4 eggs in OH forests.

Ruffed grouse mean clutch size in the Appalachian region was negatively related to incubation date. This relationship could have 2 explanations. First, ruffed grouse have relatively constant rate of egg-laying (Bump et al. 1947), thus it follows that individuals that initiated laying eggs later will have smaller clutches if counts are not standardized by nest initiation date. Due to the imprecision of estimating the exact start date of nest initiation, we were not able to standardize clutch counts in relation to nest initiation date. Given this, some clutches may have been counted before the entire clutch was laid. We are confident this was a rare occurrence because our protocol called for counting the clutch late in the incubation period (shortly before the expected hatch date) to minimize disturbance and nest abandonment and to obtain a count of the full clutch. The second explanation is that clutches laid earlier may have experienced higher rates of partial nest predation. Nest predators such as black rat snakes (*Elaphe obsoleta*) are capable of partially predating grouse nests without leaving sign or causing the female to abandon the nest and may have influenced our results.

We hypothesize that variation in mean clutch size in the Appalachian region is due mainly to latitudinal effects (i.e., latitudinal differences in length of breeding season and timing of phenological events). Despite an interspersed of MM and OH forest study areas throughout the Appalachian region we cannot ignore the influence of latitude on our estimates of mean clutch size. Three (WV1, MD1, PA1) of our 4 most northern study areas were classified as MM forest (Fig. 3), in part due to their geographic location, thus latitude was probably the primary factor in our results.

In addition to the latitudinal effect, we believe the low mean clutch size in OH forests, similar to low nesting rate, is due in part to lower quality habitat, specifically

lower quality and variable food resources. Evidence of the influence of nutrition on grouse and ptarmigan clutch size has been documented in field and laboratory studies. In a study of capercaillie using 20 years of data, Selas (2000) concluded clutch size was positively correlated with bilberry (*Vaccinium myrtillus*) production. In a laboratory study, ruffed grouse clutch size increased linearly with increasing protein ratio in their diet (Beckerton and Middleton 1982). Several studies of willow ptarmigan in Europe have correlated productivity with nutritional quality (Moss 1969, 1972, Watson et al. 1984). In a review of the influence of habitat quality on gamebird ecology, Rands (1988) concluded variation in willow ptarmigan productivity is due to variation in the quality of food available to the female and that maternal nutrition may limit grouse and ptarmigan productivity through influencing multiple aspects of reproduction including clutch size. Ruffed grouse in OH forests rely heavily on acorn production (Norman and Kirkpatrick 1984, Servello and Kirkpatrick 1987). Data collected as part of the ACGRP showed female condition prior to nesting was highly variable and body fat levels were strongly correlated to acorn production (Long et al. 2004a). In response to the low quality and variable food resources in OH forests ruffed grouse may be under selective pressure for smaller, less energetically demanding clutch sizes.

Hatchability – Our modeling effort failed to explain a meaningful amount of variation in hatchability or indicate factors that may influence hatchability. Median hatchability in the Appalachian region was 82% and was similar to most reported estimates of hatchability throughout ruffed grouse range. In New York, estimates of mean hatchability range from 94.5% (Bump et al. 1947) to 97% (Edminster 1947). Researchers in Canada reported mean hatchability rates from 87% in Ontario (Cringan

1970) to 97% in Alberta (Rusch and Keith 1971). Early studies conducted in Minnesota reported hatchability ranging from 59% - 68% (Marshall and Gullion 1965, Maxon 1978), but these studies did not incorporate radio-tagging females and may provide inaccurate estimates. We conclude the poor fit of our models was due to the relatively low variation in hatchability across individuals, study areas, forest associations, and years. Bump et al. (1947) commented on the lack of variation in hatchability (or egg fertility) and concluded losses from failed eggs (or embryonic death) play a very minor role in grouse dynamics relative to other aspects of productivity and mortality. Our findings and those of other researchers (Edminster 1947, Cingan 1970, Rusch and Keith 1971, Balzer 1995) support this conclusion.

Nest Success – Mean nest success in the Appalachian region (63% - 70% on OH and MM forests respectively) was similar to reported rates in New York (61%, Bump et al. 1947), Alberta (61%, Rusch and Keith 1971), and Minnesota (59%, Maxon 1978), but higher than rates reported in Wisconsin 43%-48% (Holzwart 1990, Balzer 1995, Small et al. 1996) and Michigan (48%, Larson 1998). The apparent difference between our estimate and that of Larson (1998) may be due to different methodology. Larson (1998) used the Mayfield method to estimate nest success, but we estimated apparent nest success by intensely monitoring radio-marked females. Larson (1998) argued that apparent nest success may over-estimate nest success by failing to identify nests that are lost early in the egg-laying or incubation periods. We believe our estimates are robust because we intensely monitored a known and individually marked population of females starting before the initiation of egg-laying. We monitored females

approximately every 1-2 days and we are confident we were able to determine the initiation of nesting behavior and subsequent nest losses.

Our modeling efforts did not clearly support 1 model for nest success, but indicated relatively equal support for 4 competing models that received greater support than the null model (Table 15). Each of these models received low model weight and had relatively low concordance scores. Model 16 received the more support than the other models and indicated nest success was influenced by the interaction between mast production the previous fall and mean minimum temperature in April and May. Nest success has been found to be positively correlated with mean minimum temperature in other studies (Hale and Wendt 1951, Swenson et al. 1994). During cold springs females may be required to feed more often and for longer periods to meet their energetic requirements. During these feeding bouts, eggs are exposed to cold temperatures and predators which may decrease hatchability and increase nest predation.

When we developed this *a-priori* model (model 16), we believed nest success would be positively correlated with mast production, assuming females in good condition would produce higher quality eggs and would have greater body reserves allowing them to spend a greater amount of time incubating and defending the clutch. Contrary to our hypothesis, nest success was negatively related to mast production in this model. Research on small mammal population dynamics has demonstrated strong correlations between mast production and small mammal productivity (McShea and Healy 2002). Small mammals, including skunks (*Mephitis mephitis*), red squirrels (*Tamiasciurus hunsonicus*), chipmunks (*Tamias striatus*), and opossums (*Didelphus*

virginianus) have been documented depredating ruffed grouse nests. The existence of a complex, ecological food web involving acorn production, small mammal populations, and ruffed grouse productivity, specifically nest success, is theoretically possible, but is beyond the scope of our data to support or refute. The structure and function of these relationships become more difficult to explain when considering the possible interaction with mean minimum temperature in April and May.

Two models (1 and 8) indicated variation in nest success was due to differences in study areas. Ascribing variation to differences in study areas does not provide insight into the biological mechanism(s) underlying the spatial variation or separate them from measurement error. Several hypotheses have been proposed to explain spatial variation in nest success including differences in age structure (Small et al. 1996), predator communities (Bergerud and Gratson 1988), nesting habitat, and nutrition. Previous research on multiple grouse species, including ruffed grouse, suggested nest success differed between juveniles and adult, and that mean nest success is influenced by the population age structure (Bump et al. 1947, Bergerud 1988, Small et al. 1996). We did not find evidence that nest success differed between juveniles and adults and conclude the observed spatial variation among study areas was not due to differences in age structure.

Spatial variation in nest success may be due to differences in predator communities (Bergerud 1988). According to this hypothesis, low nest success in the southern portion of ruffed grouse range is due to greater abundance and diversity of nest predators. Based on our data, nest success in the Appalachian region (63%) does not appear to be lower than nest success in the core of ruffed grouse range, but our

findings do not directly refute the hypothesis that spatial variation in nest success is due to differences in predator communities.

Nest success also may be influenced by micro-habitat characteristics. In New York, ruffed grouse nest success was not strongly influenced by crown cover or undergrowth density, but was correlated with distance to openings. Nests located >100 m from openings were more successful than nests located ≤ 10 m (Bump et al. 1947). In the Appalachian region, successful nests were more often located further (>100 m) from openings, in pole stands (12.5-27.8 cm dbh), and in understories with 21-60% woody and <30% herbaceous vegetation than unsuccessful nests (Tirpak and Giuliano 2004). These studies suggest spatial variation in nest success may be due, in part, to variation in the quality of nest microhabitat.

Finally, spatial variation in nest success may be influenced by the quality and availability of food resources across landscapes and between regions (Jakubas et al. 1993, Rusch et al. 2000). Our modeling exercise provided limited support that nest success differed between OH (63%) and MM forests (70%). We believe differences in forest associations are part of the biological mechanism driving site-to-site variation in nest success (as indicated in models 1 and 8) and the primary difference between OH and MM forests is the quality and availability of food resources. We propose the spatial and temporal variation observed in ruffed grouse nest success in the Appalachian region is due in part to differences in female nutritional condition between oak-hickory and mixed-mesophytic forests.

Re-nest rate – Ruffed grouse re-nesting rate, similar to nesting rate, differed substantially between OH (3%) and MM (45%) forests. Re-nesting rate on MM forests

was within the range of those reported throughout ruffed grouse range. Re-nesting rate was 22-26% in New York (Bump et al. 1947), 46% in Michigan (Larson 1988), 56% in Wisconsin (Balzer 1995, Small et al. 1996), and 61% in Alberta (Rusch and Keith 1971). In a review of ruffed grouse studies, Bergerud (1988) estimated 22-26% of grouse with failed first nests attempt a second nest. The most similar re-nesting rate to our estimate of 3% re-nesting in OH forests was reported by Maxon (1978) who reported a re-nesting rate of 14% in Minnesota.

Few studies discuss or identify potential mechanisms influencing re-nesting in ruffed grouse. Bump et al. (1947) argued that re-nesting contributed little to ruffed grouse productivity and could not compensate for high rates of nest loss. However, Bergerud (1988) theorized that grouse species initiate first nest earlier than the optimal time (in terms of environmental conditions for newly hatched chicks) to allow opportunities to re-nest. He further argued re-nesting rate is determined by the trade-off between recruitment and longevity that must be made to maximize fitness. Ruffed grouse in the Appalachians (particularly the southern portion) initiate breeding activities earlier (see discussion on incubation date) and experience longer growing seasons than grouse in the core and northern portions of their range and should, theoretically, have greater opportunities to re-nest. Yet, our results indicate re-nesting in the Appalachian region, particularly on OH forests is substantially lower than in the core range. If re-nest rate in ruffed grouse is determined by a trade-off between recruitment and longevity, then adult survival in the Appalachian regions should be higher than in the core and northern portion of grouse range and must be high enough to compensate for the reduced re-nesting. There is evidence that adult survival in the Appalachian region is

higher than in the core of ruffed grouse range (see discussion on survival) supporting Bergerud's hypothesis.

Another possibility is ruffed grouse in OH forests do not have the reserves (i.e., lipid and protein) to lay a second clutch. Research conducted as part of the ACGRP and other researchers has shown ruffed grouse nutrition and female condition differ drastically between the Appalachian region and the core of ruffed grouse range (Norman and Kirkpatrick 1984, Servello and Kirkpatrick 1987, Long et al. 2004a,b). Further, female condition mediated through nutrition influences multiple aspects of tetraonid reproduction (Moss 1969, Beckerton and Middleton 1982, Bergerud 1988, Rands 1988, Selas 2000). The possibility that difference in re-nest rate between OH and MM forests is due to differences in diet quality and availability is not mutually exclusive with Bergerud's hypothesis that grouse make a trade-off between recruitment and longevity.

Hen success - Hen success is seldom reported in ruffed grouse research, probably due to the minor contribution of re-nesting to ruffed grouse productivity (Bump et al. 1947). In the Appalachian region, hen success differed between OH (63%) and MM (70%) forests. Hen success is the cumulative result of nest rate, first nest success and re-nest rate. In the Appalachian region, nest rate and re-nest rate were lower on OH forests and MM forests. We suggest lower hen success in OH forests compared to MM forests is the result of poor female condition in OH forests during the pre-breeding and breeding periods. We posit ruffed grouse in OH forests are nutritionally stressed (Norman and Kirkpatrick 1984, Hewitt and Kirkpatrick 1996, Servello and Kirkpatrick

1987, Long et al. 2004a,b) and do not have the necessary reserves (i.e., proteins and lipids) to nest every year or re-nest in most years.

Chick Survival – Chick survival (22%) in the Appalachian region to 35-days post-hatch was extremely low compared to other portions of ruffed grouse range. However, we note that our estimates should be considered minimum estimates due to the possibility of under counting chicks during flushes. Chick survival to brood break up (≈ 82 days) was 33% in Minnesota (Marshall and Gullion 1965) and 51% in Alberta (Rusch and Keith 1971). In New York, estimated mean chick survival to August (≥ 77 days) was 40% (Bump et al. 1947). Beckerton and Middleton (1982) estimated that chick survival to 56-days post-hatch in Ontario was 78%. Early estimates of chick survival (Bump et al. 1947, Marshall and Gullion 1965, Rusch and Keith 1971, Beckerton and Middleton 1982) were based on observation of unmarked broods and could not account for entire brood losses, thus probably over-estimated chick survival. In a recent study in Michigan, researchers placed radio-transmitters on 6-day old chicks and estimated survival during a 12-week period was 32% (Larson et al. 2001). Again, this study indicated a much higher survival rate than we observed in the Appalachian region, but this estimate may have also been biased high as ruffed grouse chick mortality is highest in the first week after hatch (Bump et al. 1947, Smith et al. 2004).

Dobson et al. (1988) concluded female nutritional condition was 1 of 2 primary factors influencing gamebird chick survival, the other being the availability of insects for newly hatched chicks. Our results indicated a positive relationship between chick survival and hard mast production the previous fall which supports this hypothesis. Furthermore, several researchers working with multiple species of tetraonids have

drawn similar conclusions (Jenkins et al. 1967, Moss 1969, Miller et al. 1970, Watson and O'Hara 1979, Hewitt and Kirkpatrick 1996, Beckerton and Middleton 1982). Long-term research on red grouse (*Lagopus lagopus*) in Europe indicated females feed selectively on portions of heather (*Calluna vulgaris*) that are rich in nitrogen and phosphorus (Moss 1972, Lance 1983). Further, experimental studies have demonstrated red grouse productivity is higher on areas with higher quality heather (Miller et al. 1970, Watson et al. 1984). These studies support the "indirect nutrition hypothesis" (Watson and Moss 1972), which argues that tetraonid egg quality and chick viability (i.e., survival) is determined by the nutritional condition of the adult female. In species with precocial young, newly hatched chicks absorb the remaining yolk from the egg which serves as the primary energy source during the first few critical days of life. Females in poor nutritional condition lay lower quality eggs which have smaller yolks and provide less energy for newly hatched chicks (Welty and Baptista 1988). Females in good nutritional condition lay higher quality eggs with larger yolks and greater energy reserve for newly hatched chicks. The amount of yolk available to the newly hatched ruffed grouse chicks is critical because chicks leave the nest within 24-hours and, perhaps most importantly, ruffed grouse chicks cannot thermoregulate for the first 7-days post-hatch. During periods of inclement weather chicks must be brooded by the female and cannot forage, thus they must rely on the yolk reserves to meet their energy requirements.

Though the fit ($R^2 = 0.04$) of model 25 which indicated chick survival was influenced by mast production the previous fall was low it was the only model supported in the selection process. Given the coarseness of our mast evaluation procedure, we

believe our results indicate fall mast production (mediated through female condition) is 1 mechanism influencing chick survival in the Appalachian region. Complimentary research conducted as part of the ACGRP showed percent carcass fat of female ruffed grouse was positively related to mast production in the fall and the presence of acorns in the crop in late winter (Long et al. 2004a). Additionally, chick survival to 35-days post-hatch was positively correlated with the amount of carcass fat in females (Long et al. 2004a). Study areas where females had low mean fat levels had lower chick survival rates to 35-days post-hatch (13%) compared to areas with moderate (37%) and high (26%) fat levels (Long et al. 2004a). We posit that, in years of poor mast production, chick survival is low (regardless of environmental conditions) due to poor quality eggs (i.e., small yolk sizes) and weak chicks. In years of above average mast production chick survival may be higher (depending on environmental conditions) because chicks are hatched from high quality eggs with relatively large energy reserves in the form of remaining yolk. In years of average mast production, we believe other environmental factors, specifically temperature and precipitation have greater influence on chick survival. However, we did not investigate the influence of brood habitat availability, quality or selection on chick survival and cannot assume low chick survival is not influenced by ≥ 1 aspects of brood habitat.

Survival Analysis

We obtained multiple estimates of annual and seasonal survival rates using 2 methods and different subsets of the ACGRP database. Based on the Kaplan-Meier staggered entry method, ruffed grouse mean annual survival in the Appalachian region

was 42%, but ranged from 17% – 57% across study areas. Using the known-fates model with covariates annual survival ranged from 44% - 53% across years.

Our estimates of ruffed grouse annual survival in the Appalachian region were slightly higher, but within the range of previous reported rates from the core of ruffed grouse distribution. Mean annual adult survival was 42% and 50% on 2 study areas in New York (Bump et al. 1947), and 45 - 66% in Minnesota (Gullion and Marshall 1968). Estimates of annual survival in Wisconsin range from 25% (Small et al. 1991) to 34% (Dorney and Kabat 1960). In Minnesota annual survival was 1% and 21% for gray- and red-phased birds respectively (Gutierrez et al. 2003). Rusch and Keith (1971) reported that annual survival in Alberta was 27 – 30%. Survival ranged from 25-37% on areas opened and closed to hunting in Michigan (Clark 2000). Notably, previous research conducted in the Appalachian region produced similar estimates of annual survival. Annual survival was 47% in Ohio (Swanson et al. 2003) and 62% in Kentucky (Triquet 1989).

Observed trends of ruffed grouse seasonal survival in the Appalachians were similar to patterns reported throughout ruffed grouse range. Survival was highest in summer and lowest in winter. Across our model sets, summer survival ranged from 93% to 94%, spring survival from 75% to 92%, fall survival 74% to 83%, and winter survival 72% to 84%. Our estimates were similar to other seasonal survival rates reported in the Appalachian region (Triquet 1989, Swanson et al. 2003). However, our estimates of seasonal survival rates were higher than rates reported from the core of ruffed grouse range. In central Wisconsin, adult and juvenile summer survival was 85% and 65% respectively, spring survival was 73% and 50% respectively, fall survival was

65% and 48% respectively, and winter survival was 57% and 55% respectively (Small et al. 1991). Winter survival of grouse translocated to Tennessee was 45% (White and Dimmick 1978). Overwinter survival in Alberta was 42% and 67% in 1967 and 1968, respectively (Rusch and Keith 1971). Ruffed grouse seasonal survival in New York was highest in summer and lowest in winter (Bump et al. 1947).

Causes of ruffed grouse mortality in the Appalachian region were similar to those reported throughout the range of ruffed grouse (Bump et al. 1947, Marshall and Gullion 1965, Rusch and Keith 1971, Rusch et al. 1978, Small et al. 1991, Swanson et al. 2003). Predation accounted for 84% of all known mortalities. Avian predators were the leading cause of predation, followed by mammalian predators, and unidentified predators. Mortality agents were determined by inspection of carcass remains and sign surrounding the relocated carcass or radio-collar, but Bumann and Stauffer (2002b) concluded scavenging by mammalian predators altered field evidence, thus our results represent a minimum estimate of avian predation and a maximum estimate of mammalian predation. In the core of ruffed grouse range northern goshawks (*Accipiter gentilis*) and great horned owls (*Bubo virginianus*) are considered the primary predators of ruffed grouse, but goshawks are rare in the Appalachian region (Bumann and Stauffer 2004); the primary predators in the Appalachians are the Cooper's hawk (*Accipiter cooperii*) and owls (Bumann and Stauffer 2004). Avian predation rates increased during fall and spring raptor migrations (Bumann and Stauffer 2004).

Harvest accounted for a smaller portion (12%) of all known mortalities compared to previous studies. Harvest accounted for 13% to 20% of known mortalities in New York (Bump et al. 1947), 28% (Small et al. 1991), 40% (DeStefano and Rusch 1986) in

Wisconsin, and 19% to 48% in Alberta (Fischer and Keith 1974). Swanson et al. (2003) concluded harvest (8.6% of known mortalities) was a minor source of grouse mortality in Ohio.

Factors influencing survival – Our results indicated several factors influence ruffed grouse survival in the central and southern Appalachian region (Table 43). Further, our results indicate adult annual survival is higher in OH forests than in MM forests. In a review of grouse ecology, Bergerud and Gratson (1988) argued grouse exhibit 2 mortality modes. The “low mortality mode” is characterized by annual mortality rates $<45\%$ (or annual survival $\geq 55\%$) and the “high mortality mode” is characterized by annual mortality rates $>45\%$ (or annual survival $\leq 55\%$). They also noted the ruffed grouse exhibit both modes throughout its range. Our estimates suggest grouse in OH forests exhibit the low mortality mode and grouse in MM forest exhibit the high mortality mode.

Bergerud and Gratson (1988) proposed 2 hypotheses to explain the presence of high and low mortality modes. The “predator/cover” hypothesis posits that grouse survival rates will be higher if the population(s) of effective predator(s) are reduced or absent. Throughout most of ruffed grouse range, that most effective predator is the northern goshawk, but, goshawks are rare in the central and southern Appalachian regions. During the course of the ACGRP, field personnel reported only 5 sightings of goshawks each during fall or spring migration (Bumann and Stauffer 2004). Our estimates of higher adult survival in the Appalachian region and the lack of goshawks in the region support the “predator/cover” hypothesis, but this hypothesis cannot explain the observed differences between OH and MM forests. Goshawks are not present in

either forest association in the Appalachian region, thus differential survival between forest associations must be due to 1 or more other factors.

The second hypothesis presented by Bergerud and Gratson (1988) argues differences in high and low mortality modes are due to differences in reproductive risks. Specifically, females with smaller clutches have lower reproductive risks and higher survival than females with larger clutches. An important limitation of this hypothesis is that it only applies to females. Further, Bergerud and Gratson (1988) could not find published results to support this hypothesis. Despite these limitations, our results provide limited support that differential reproductive risks may result in differential adult survival. Female grouse in OH forests had lower nesting rate, nest success, re-nest rate, clutch size, and chick survival than female grouse in MM forests, but also exhibited higher adult survival.

The influence of age on ruffed grouse survival is unclear. We conducted our survival analyses using multiple time scales (i.e., 5-years, 1-year, and 3-months) and each analysis used a different subset of the ACGRP data base. In our analysis of survival from April 1997 – March 2002, we used age at capture as a covariate, but we did not find evidence that age at capture influenced survival during the 5-year period. There are 2 possible explanations for this finding. First age may not influence ruffed grouse survival in the Appalachian region. Second, the influence of age may have been obscured because we used only 2 age classifications (juvenile and adult) and juveniles surviving >1 year were not graduated to adults. This classification system limits our ability to investigate more complex age structure. Specifically, if the functional

relationship between age and annual survival is actually a quadratic form, then fitting a linear model with 2 age classes would indicate survival is not influenced by age.

In contrast, our analyses of 1-year datasets (i.e., 1997 – 1998, 1998 – 1999, etc.) accounted for graduating juveniles to adults, yet age was not an important factor in ruffed grouse survival. Only in 1998 – 1999 and 1999 – 2000 was age included in any of the competing models (i.e., $\Delta_i \leq 2.0$). In each case, the 95% confidence intervals on the beta estimate for age overlapped 0.0 indicating age had a weak or non-existing influence on survival.

We also conducted season-specific analyses (using a monthly time step) and assumed each season (i.e., fall 1997, fall 1998, fall 1999, etc) was independent. In these analyses juveniles surviving >1 year were graduated to adults and may have been included in >1 group. For example, an individual bird may have been classified as juvenile in fall 1998, survived to the next fall and then graduated to an adult. This bird would have been included in the fall analysis as 2 individuals, a juvenile in fall 1998 and an adult in fall 1999. We found evidence that adult grouse had higher survival in fall (2% greater) and winter (4% greater) than juveniles. Yet, competing models suggested age did not influence survival. Several explanations may explain our model results. First, adults do have higher survival in fall and winter than juveniles, but the difference is small. Second, some individual birds are genetically superior and have greater longevity than others. These birds would be included in multiple season and year groups and may create a biased sample. In this situation, it is not necessarily age that improves survival, but genetics. As the study progressed these individuals may have composed a greater proportion of the sample. An assumption of survival studies is

independence among individuals (Pollock et al. 1989b). Ideally, researchers would maintain ≥ 30 radio-marked animals at any given time and censor birds surviving at the end of each year. Each subsequent year would begin with a new cohort of individuals. Due to the low abundance of ruffed grouse in the Appalachian region we were unable to censor surviving birds at the end of each year and start with a new cohort. Including individuals over time may have biased our assessment of the influence of age on ruffed grouse survival.

The literature does not clarify the relationship between age and survival. Adult ruffed grouse in Wisconsin (Small et al. 1991) and Alberta (Rusch and Keith 1971) had higher survival than juvenile ruffed grouse. In contrast, juvenile ruffed grouse had higher survival than adults in Michigan (Clark 2000). Research in Minnesota (Gutierrez et al. 2003), Ohio (Swanson et al. 2003), and Kentucky (Triquet 1989) concluded survival did not differ between adults and juveniles. We suggest age has a minor influence on ruffed grouse survival and probably operates only during short windows, specifically early fall (e.g., September). Further, the influence of age on survival varies temporally and spatially which would explain the contrasting results in our study and in the published literature. We suggest variation in extrinsic factors (e.g., weather conditions, predator composition and abundance) and intrinsic factors (e.g., female condition in spring) more strongly influences juvenile than adult survival and will cause juvenile survival to differ from adult survival in some years and some locations. Additionally, measurement error due to sample size and composition influences results and can obscure the true relationship between ruffed grouse age and survival.

Similar to age, the influence of sex on ruffed grouse survival is debatable. Our analysis of the 5-year data set and annual data sets overall indicated survival did not differ between males and females. Our analysis of spring survival indicated males had higher survival than females. Several studies conducted throughout ruffed grouse range have concluded ruffed grouse survival does not differ between males and females (Rusch and Keith 1971, Gutierrez et al. 2003, Swanson et al. 2003). However, male ruffed grouse were more vulnerable to harvest mortality in Michigan (Clark 2000). Hannon et al. (2003) concluded male willow ptarmigan have higher survival than females. Bergerud (1988) argued males and females have different mortality regimens due to difference in reproductive investments. Male reproductive investment for most grouse species, including ruffed grouse, is limited to advertising for females. Females have a much greater investment in reproduction including defending nests and caring for young and experience higher mortality during the reproductive season than males. Others have argued displaying males are at greater risk of predation from aerial predators and may have lower survival during the spring than females. We suggest the influence of sex on survival operates during a very short window in spring and varies temporally and spatially. During the course of the year, the influence of sex on survival in the Appalachian region is probably a minor component.

Test of the Compensatory Mortality Hypothesis

The compensatory mortality hypothesis was first proposed in the 1930s (Errington and Hamerstrom 1935). Since then, it has been the focus of numerous studies and debates. Our results indicated ruffed grouse survival did not increase in the absence of hunting, suggesting ruffed grouse harvest mortality in the Appalachian

region is compensatory (regardless of sex or age). We caution researchers and managers to interpret our findings carefully and conservatively. We must consider several issues when interpreting our results, including the study design and power, and conflicting conclusions in the published literature.

An important limitation in wildlife research is our ability to conduct controlled, replicated field experiments that can falsify hypotheses (Romesburg 1981). The ACGRP was an uncommon project in wildlife research because of its experimental design, geographic scale and duration. Our study design was based on a completely randomized block design with repeated measures, but due to financial, logistical, and political constraints we were faced with several limitations in the execution of the test of the compensatory mortality hypothesis. First, we had a small sample (4 control and 3 treatment areas). We did not use data from 5 study areas because complete data were not collected during phase I (1996-1999) and phase II (1999 – 2002) of the study. Considering the inherent variation among study areas and years, and our small sample size, we suggest the test statistic for the phase*treatment interaction ($F_{1,18} = 2.11$, $P = 0.1335$) should be interpreted conservatively and that $\alpha = 0.1$ would be a reasonable benchmark for interpreting our results.

Second, due to political constraints, we were unable to *randomly* assign treatments (open or closed to hunting) to each of the study areas. Because we were not able to randomly apply the treatments, we decided to apply the largest “effect” possible and elected to close hunting on the 3 study areas (VA3, WV1, KY1) with the highest harvest rates during phase I (1996, 1997, and 1998). Our reasoning was to apply the largest treatment possible and that if we were to detect no effect from

removing hunting from study areas with the highest harvest rates, a hunting effect likely did not exist. The most important consequence of this non-random process is that we cannot draw inference beyond our study areas and period of study, nor can we infer a cause and effect relationship.

Finally, harvest rates experienced during our study were lower than reported in other parts of ruffed grouse range. The mean harvest rate on control areas was 8% (range 4 – 13%). Mean harvest rate on treatment areas prior to closure (during 1997 – 1998 and 1998 – 1999) was 20%. In comparison, mean ruffed grouse harvest rates in New York ranged from 13 – 20% (Bump et al. 1941) and 29 – 50% in Wisconsin (DeStefano and Rusch 1986, Small et al. 1991). Others have suggested maximum allowable harvest rates for ruffed grouse are 25% (Edminster 1947), 30 – 35% (Dorney and Kabat 1960), 40% (Palmer 1956), and 50% (Palmer and Bennet 1963). Importantly, annual harvest rates declined on control areas from 1997 to 2000 and increased to the end of the study (Fig. 12). The low harvest rates, particularly on control areas, experienced during this study reduced the potential effect size and potential power of our experiment.

Studies investigating the effect of hunting on tetraonid species in North America and Eurasia have produced equivocal results. Several studies support the additive mortality hypothesis. A mean harvest rate of 44% (range 23 – 72%) was additive to natural mortality and reduced ruffed grouse densities in Wisconsin (Kubisiak 1984). During a long-term banding study of blue grouse (*Dendragapus obscurus*) harvest mortality of females was determined to be additive (Zwicker 1982).

Other studies suggest harvest mortality is compensatory up to a threshold and then becomes additive, this pattern is referred to as either partially additive or partially compensatory. In New York, researchers experimentally harvested 19.5%, 20%, and 13.4% of the fall population on 1 study area and compared over-winter survival to an adjacent reference area in 3 consecutive years. Over-winter survival was 45.2%, 55.8%, and 65.8% on the hunted area compared to 39.1%, 43.4%, and 60.5% on the reference area (Bump et al. 1947). The authors concluded decreases in natural mortality rates could compensate for 50% of harvest mortality and harvest mortality is a minor component in ruffed grouse population dynamics (Bump et al. 1947). Recently, researchers in Norway conducted a similar test of the compensatory mortality hypothesis by experimentally harvesting 0%, 15%, and 30% of willow ptarmigan on 13 study areas during a 4-year study. Willow ptarmigan exhibited density-dependent growth rate, but the researchers concluded harvest mortality was partially additive and only 33% of harvest mortality was compensated for by changes in natural mortality (Pedersen et al. 2004). In central Wisconsin, ruffed grouse harvest mortality was higher on public than private land for juveniles (0.56 vs. 0.09 respectively) and adults (0.73 vs. 0.13), yet mortality rates outside the hunting seasons were similar (0.80 vs. 0.77) indicating harvest mortality was at least partially additive on public lands (Small et al. 1991). In Wisconsin, ruffed grouse captured <201 m from an access trail experienced higher harvest rates (48%) and lower annual survival (23%) than birds captured >201 m from the road (19% and 36% respectively) suggesting harvest mortality was partially additive for birds captured <201 m from access trails (Fischer and Keith 1974). They suggested the reduction in natural mortality rates could compensate for 41% of the

harvest mortality (Fischer and Keith 1974), however there was no correlation between ratios of population change (October – May) and harvest rate, indicating fall hunting may have been compensatory (Fischer and Keith 1974).

Numerous studies have concluded harvest mortality is compensatory. In western North Carolina, grouse abundance did not differ before, during, or after hunting season in small woodlots with 3 levels of prescribed hunting pressure (no hunting, moderate hunting, and unrestricted hunting, Monschein 1974). Though this study was based on flush counts of unmarked birds, later researchers have drawn similar conclusions. Gullion and Marshal (1968) concluded 18% harvest of territorial male ruffed grouse was compensatory. Others in Wisconsin suggested harvest mortality <40% of preseason population is compensatory (Dorney and Kabat 1960). Experimental research on red grouse provided similar results suggesting 30% of harvest can be compensated for by changes in natural mortality (Jenkins et al. 1963). In Ohio, harvest accounted for 8.6% of mortalities and was determined to be compensatory (Swanson et al. 2003). Harvest mortality was also determined to be compensatory in Michigan (Clark 2000). Harvest of male black grouse ($\leq 57\%$) in the southern French Alps influenced the age ratio of males, but did not influence reproductive success or cause a decline in abundance (Ellison 1978).

A common factor in studies concluding either partial or complete compensation of harvest mortality was the role of immigration. Many studies have compared demographic rates and densities on hunted and non-hunted sites, but the results are not conclusive because the populations were not closed. By comparing spring densities between hunted and non-hunted areas, researchers concluded 40% removal of the fall

population of rock ptarmigan did not influence spring densities (McGowen 1975). These results suggested harvest mortality was compensatory, but the authors argued that immigration to the hunted areas was an important part of the apparent compensatory response. Researchers drew a similar conclusion about white-tailed ptarmigan populations in Colorado. Though mortality rates were higher on hunted than non-hunted areas in Colorado, immigration apparently maintained stable spring densities on hunted areas (Braun and Rogers 1971, cited in Bergerud 1988). Immigration was also cited as supporting willow grouse populations on hunted areas in Norway (Myrberget 1985). A similar study on ruffed grouse concluded immigration supported grouse populations on hunted areas (Palmer and Bennet 1963). Fischer and Keith (1974) showed ruffed grouse trapped <201 m from access trails experienced higher harvest rates than ruffed grouse trapped >201 m from access trails. This finding is easily explained by hunter behavior, in Michigan, Maine, and Wisconsin where most ruffed grouse hunting occurs within 402 meters of roads (Gullion 1983). It is probably safe to assume this pattern holds throughout the range of ruffed grouse. These studies support Gullion's (1983) argument that inaccessible areas (or limited access areas) can serve as refugia for ruffed grouse and supply surplus birds to areas that experience high hunting pressure.

We conclude that harvest rate $\leq 20\%$ in the southern and central Appalachian region is compensatory. However, we stress our results ($P = 0.133$) merit caution in concluding harvest mortality is not additive and that higher harvest rates may be additive. We believe current harvest rates can be maintained, but regional state agencies should not amend hunting seasons to facilitate higher harvest rates. It is

critical to recognize our results are not conclusive due to limitation in sample size and effect size; we cannot assume harvest rates higher than those observed in this study are compensatory, nor can we extrapolate our results beyond the Appalachian region.

Although we believe regulated sport harvest did not have a direct impact on ruffed grouse survival, there is evidence that disturbance from hunting (and other activities) influenced habitat selection and home range size of ruffed grouse in the Appalachian region (Whitaker 2003). Ruffed grouse (regardless of sex and age classes) made greater use of clearcuts and mesic bottomlands and had smaller home ranges in the absence of hunting (Whitaker 2003). We believe this type of disturbance deserves consideration in the development of ruffed grouse hunting regulations and land management plans (see management implication section).

Population Modeling

Our modeling exercise provided widely variable estimates of λ between models and across spatial scales (Table 40). These results raise 2 questions; why are the estimates different and which model is more accurate? We believe the difference in estimated λ between models 1 and 2 is due to differences in estimated fecundity (the number of chicks raised to 35-days post-hatch per female alive on 1 April; Table 40) which determines the number of chicks entering the fall population and drives the resulting estimate of λ . Further, we believe the difference in estimated fecundity between models 1 and 2 is due to the amount and structure of measurement error and covariance incorporated in each model.

In model 1, fecundity was the function of multiple reproductive parameters (i.e., nest rate, nest success, re-nest rate, etc.) each of which introduces measurement error

resulting in increased variation around the mean estimate of fecundity. Previous research has demonstrated a negative relationship between the amount of variation in a system and the predicted mean response. In other words, as variance increases the mean estimate decreases. The increased variation due to multiple reproductive parameters explains, in part, why our estimates of fecundity and λ were so low in model 1. In contrast fecundity in model 2 was reduced to 1 parameter thus potentially decreasing measurement error and variation.

Secondly, in model 1 we did not incorporate covariance among the reproductive parameters. However, it is highly probable in nature that reproductive parameters do co-vary. For example, following a good mast crop we would expect nest rate, re-nest rate, and chick survival to all increase. The opposite is true in years of poor mast production. Failure to account for covariation among reproductive parameters would also increase the variation in the system and bias our estimate of fecundity low. Again, by estimating fecundity with 1 parameter in model 2 reduced overall variation and probably produced a more accurate estimate of fecundity.

Considering the differences (i.e., measurement error, covariance, and variation) between models 1 and 2, we believe model 2 is the more accurate and reliable model because it is more parsimonious. Furthermore, the estimate of mean λ (at the regional scale) from model 2 is much more similar to the estimate derived from breeding bird survey data (Sauer et al. 2004), the only independent data that provides a useful comparison. These findings provide a level of confidence that the model structure and parameter estimates from model 2 are reflective to a certain degree of ruffed grouse population dynamics in the southern and central Appalachian region.

Mean estimates of λ based on our stochastic model differed slightly between the deterministic and stochastic models. We believe the differences were due to the assumed distributions (e.g., uniform distribution of mast production) used in the stochastic model. Despite the minor differences in point estimates, the stochastic model (and model 2) provided similar results and indicated ruffed grouse populations are declining at the regional, mixed-mesophytic forest, and mixed-mesophytic site levels. Population viability at each of these scales was low (Table 42) due to low λ and high variability (Fig. 15). However, ruffed grouse populations appear to be increasing at the oak-hickory forest and oak-hickory site spatial scales.

Prior to developing the population models we anticipated λ would be higher in mixed-mesophytic forests than in oak-hickory forests. There are at least 2 possible explanations for the apparent high growth rate in oak-hickory versus mixed-mesophytic forests. First, it is possible that the increased adult survival in oak-hickory forests is enough to compensate for decreased fecundity and result in a higher mean λ . The second explanation is that our assumption about the relationship between hard mast production and fecundity is incorrect. Based on our reproductive analysis we modeled fecundity as a function of mast production the previous fall in both mixed-mesophytic and oak-hickory forests. However, it is possible that fecundity in mixed-mesophytic forests is not as strongly related to hard mast production as in oak-hickory forests due to the presence of high quality, consistently available food resources such as aspen, cherry and birch. If this is true we would expect to see less variation in mixed-mesophytic forests from year to year and thus a higher mean fecundity rate. If this is true then we underestimated fecundity and λ in mixed-mesophytic forests. Again, we

did not expect to see higher λ in oak-hickory forests than in mixed-mesophytic forests and believe additional research is needed to improve our understanding and estimates of ruffed grouse fecundity in each forest association.

Ruffed grouse population growth rate in the central Appalachian region was most strongly influenced by productivity (i.e., chick survival, model 1; Fig. 13 and fecundity, model 2, Fig. 14). Both models also indicated adult winter and fall survival (Figs. 13 & 14) had relatively moderate influence on λ . Similarly, sharp-tailed grouse population growth rate in Alberta was most strongly influenced by productivity, particularly nest success (Manzer 2004). Our results indicate management agencies will be able to increase ruffed grouse abundance most efficiently by focusing management efforts at increasing fecundity, particularly chick survival. This could be accomplished through a variety of silvicultural practices that maximize the interspersed of nesting cover, brood cover, adult escape cover, and food resources on the landscape (see management implications).

Elasticity analyses indicate which demographic parameters have the greatest influence (in theory) on λ , but in reality, managers may not have the ability to manipulate certain parameters due to biological or logistical limitations. Results from our elasticity analyses suggested managers could increase ruffed grouse population growth effectively by increasing fall and winter survival. However, we believe it is not biologically or logistically possible to increase fall and winter survival. First, our estimates of adult seasonal survival were higher than other published rates and we assume are at or near to the maximum survival rate for ruffed grouse in the wild. Second, our results indicated harvest mortality was compensatory, thus changing

harvest regulations will not result in higher adult survival. In this situation, we feel there are few management alternatives available to increase adult survival. Avian predation is the leading cause of mortality, but control of avian predators is not legal, ecologically sound, or socially acceptable. Timber management that increases the amount of early-successional, high-stem density stands may increase ruffed grouse density if there is a concurrent increase in productivity, but probably will have limited effect on adult survival. Given this situation, we feel the critical limiting factor to ruffed grouse population growth in the southern and central Appalachians is productivity.

The elasticity analyses indicated that a 60% (from 22% to 35%) increase in mean chick survival could stabilize ruffed grouse populations in the region. However, our model results of hypothetical management suggest silvicultural activities designed to increase mean annual mast production could not increase chick survival by 60% and alone will not be sufficient to stabilize ruffed grouse populations. However, this represents a minimum influence on ruffed grouse population growth because we assumed increased mast production would influence only chick survival. It is probable that increased hard mast production would have positive impacts on other aspects of reproduction including nest rate, nest success, re-nest rate, and clutch size (Moss 1969, 1972, Watson et al. 1984, Beckerton and Middleton 1982, Rands 1988, Nager et al. 2000, Selas 2000, Reynolds et al. 2003, Verbove et al. 2003). Further, chick survival may be improved through other forms of habitat management that we did not investigate. Increased hard mast production may increase adult survival, though our analyses did not provide clear evidence of a correlation between mast production and adult survival.

Models are simplified representations of complex systems (Starfield 1997); consequently, model results must be interpreted cautiously. We made explicit assumptions concerning the distribution of each demographic pattern based upon empirical data (Table 6). However, our sample sizes for particular spatial scales and parameters were often small. If the assumed distributions are not reflective of the true distributions, model results and implications will be incorrect. Second, we assumed a 1:1 sex ratio at hatch and in the adult population. Violation of this assumption could result in over- or under-estimating λ depending on the true sex ratio. Third, we assumed chick survival from 35-days post-hatch to brood breakup (approximately 84 days post-hatch) was 100%. The consequence of violating this assumption would be an over-estimate of recruitment into the fall population and possibly λ . Yet, our estimates of λ were similar to estimates from the breeding bird survey which suggests our models (deterministic and stochastic) yielded valuable and reliable insight in ruffed grouse population dynamics in the southern and central Appalachian region. We conclude regional ruffed grouse populations are declining slowly, but growth rates vary across the region. Our modeling efforts highlighted the need to improve our estimates of fecundity and recruitment and to develop long-term monitoring programs to obtain indices of population size and recruitment. Long-term indices will provide an important independent data that could be used to develop and test future predictive population growth models

Population ecology

Species may exhibit 1 or more population structures throughout their range, including clinal variation, geographic isolates, or hybrid belts (Mayr 1970). Species with

relatively contiguous populations that exhibit gradual changes in multiple characteristics throughout their distribution exemplify clinal variation (Mayr 1970). These gradual changes are adaptations to local conditions that maximize individual lifetime fitness and result in local populations that may differ slightly from others in terms of morphology, physiology, behavior, and ecology (Mayr 1970). We suggest our results, and those of others, indicate ruffed grouse from the Appalachian region north into the core of ruffed grouse range exhibit clinal population structure.

Evidence of clinal variation in ruffed grouse populations include changes in morphology, physiology, activity patterns and habitat selection, and population dynamics. Ruffed grouse have 2 dominant color phases, gray and red, which are sympatric throughout most of their distribution (Rusch et al. 2000), but only the red phase occurs in the southern and central Appalachians. During the ACGRP, gray and red phase birds were captured on the PA1 and RI1 study areas, whereas only red phase birds were captured on study areas south of PA1 (ACGRP unpublished data). Ruffed grouse also exhibit gradual changes in physiology. For example, on average, ruffed grouse in the central and southern Appalachians have greater percent body fat in early-spring than ruffed grouse from the Great Lakes region (B. Long, West Virginia University, unpublished data). Behaviorally, ruffed grouse in the southern and central Appalachian region spend more time active (i.e., foraging) during the day and less time roosting (Hewitt and Kirkpatrick 1997). In addition, ruffed grouse home range size and selection for “preferred” habitat features were strongly related to hard mast production in oak-hickory forests typical of the southern Appalachians, but not in mixed-mesophytic forests typical of the northern Appalachians (Whitaker 2003). Gradual changes in

ruffed grouse population dynamics across their range were also observed. Ruffed grouse in the southern and central Appalachians do not exhibit the 10-year population cycle characteristic of populations in the core of the species range. Similar to changes in home range size and habitat selection, we observed changes in ruffed grouse population dynamics between oak-hickory and mixed-mesophytic forests of the Appalachian Mountains (Table 44).

We posit the clinal variation in ruffed grouse population ecology from the southern Appalachians north into the Great Lakes region is due to changes in life-history strategies (i.e., different trade-off between reproduction and survival) to maximize lifetime fitness. Furthermore, we hypothesize that changes in life-history strategies are a response to gradual changes in selective pressures acting upon grouse populations as forest structure and composition changes from the southern Appalachians to the northern United States and southern Canada. Bergerud (1988) discussed examples of similar inter- and intra-specific differences in life-history strategies of several grouse and ptarmigan species over large spatial areas.

Specifically, the dominant oak-hickory forest association of the southern and central Appalachians gradually gives way to mixed-mesophytic and northern hardwood forests in the northern Appalachians and Great Lakes region (Braun 1950). These dominant forest associations differ in several aspects, but perhaps the most important difference is in the quality of food resources available to ruffed grouse (Norman and Kirkpatrick 1984, Long et al. 2004b). We believe food quality and availability may be the minimum limiting factor affecting ruffed grouse populations in oak-hickory forests of the southern and central Appalachians. Multiple aspects of ruffed grouse ecology in

oak-hickory forests appear to be related to hard mast production including habitat selection (Whitaker 2003), pre-breeding body condition (Long et al. 2004a), and reproduction and recruitment (see results and discussion). Additionally, several authors have concluded food availability and quality are key factors influencing reproduction in grouse and ptarmigan (Watson and Moss 1972, Swenson et al. 1994, Watson et al. 1998). However, hard mast production is extremely variable from year to year (Healy 1997). In years of poor hard mast production ruffed grouse must feed on low quality and potentially toxic food items (Servello and Kirkpatrick 1987). We believe ruffed grouse experiencing these conditions in oak-hickory forests favor adult survival over reproduction. This would explain why we (and others) have observed lower reproductive rates and higher adult survival rates in the Appalachian region compared to the core of ruffed grouse range. In contrast, food availability and quality does not appear to be a limiting factor in mixed-mesophytic or northern hardwood forests due to the presence of high quality, consistent, and easily accessible food items such as aspen, cherry, and birch. Thus, we believe individual grouse in mixed-mesophytic and northern hardwood forests maximize lifetime fitness by favoring reproduction over adult survival. We note that food availability and quality are not the only factors influencing ruffed grouse populations in the central and southern Appalachians, but believe it may be the current minimum limiting factor (Leopold 1933). In addition to gradual changes in food resources, we believe changes in climatic conditions (i.e., snowfall and accumulation patterns, Gullion 1970), brood habitat (Smith et al. 2004), and predator communities (Bump et al. 1947, Gullion 1970) may contribute to spatial variation in ruffed grouse population ecology and life-history strategies.

Management Implications

Our results indicated ruffed grouse populations in the southern and central Appalachians have lower productivity, but higher survival than populations from the core of ruffed grouse range (Table 44). Our results further showed ruffed grouse productivity is influenced by hard mast production in the fall and harvest mortality is compensatory (at current levels). Though our modeling efforts indicated increasing adult survival during fall and winter would have a strong influence on population growth rate, we feel increasing survival is neither biologically or logistically feasible for several reasons. First, because of the high adult survival rates observed in the central and southern Appalachian region (this study, Triquet 1989) we believe it is not biologically possible to increase survival much above the currently observed rates. Second, if we accept that harvest mortality (at the harvest rates observed in this study) is compensatory on an annual basis, we are left with few management alternatives to increase survival. Avian predation was the leading cause of adult mortality, but control of avian predators is not an option (ecologically, ethically, or legally), nor could we expect it to result in increased ruffed grouse abundance (Bump et al. 1947). Habitat management, specifically timber management may increase adult survival by creating escape cover, but we cannot make the determination based on our data.

To increase ruffed grouse abundance and maintain hunting opportunities in the central and Appalachian region we recommend focusing efforts on habitat management designed to increase productivity by increasing food abundance and interspersing nest and brood cover among early-successional stands. We also recommend ruffed grouse harvest plans focus on providing high quality hunting opportunities and not increased

harvest rates. Finally, we recommend implementing monitoring programs to obtain population indices that can be used to develop and or validate predictive population models. The following discussion and recommendations for ruffed grouse management in the Appalachian region are based on ecological considerations and assumes an area is being managed specifically for ruffed grouse. Other considerations including habitat needs for other wildlife species, sociological (i.e., recreational opportunities and aesthetics), and financial constraints must be balanced with our recommendations.

Food resources – The results of this and other studies (Norman and Kirkpatrick 1984, Servello and Kirkpatrick 1987, Hewitt and Kirkpatrick 1997, Whitaker 2003, Long et al. 2004a,b) suggest ruffed grouse in the Appalachian region, and particularly in oak-hickory forests are nutritionally stressed. The nutritional limitation experienced by ruffed grouse in the region influences home range size and selection of preferred habitat features (Whitaker 2003), physiology (Long et al. 2004a), and population dynamics (this study). Therefore, we believe a primary goal of land management should be to increase the abundance and availability of food resources. Acorn production from red and white oak species appears to be the most important ruffed grouse food resource in the Appalachian region (Norman and Kirkpatrick 1984, Servello and Kirkpatrick 1987), consequently land managers should pursue silvicultural practices that can increase acorn production. Whitaker (2003) provides a detailed review of silvicultural practices designed to increase acorn production and provide other aspects of ruffed grouse habitat requirements. In essence, early-successional forest stands that provide escape cover and food resources can be created using clearcuts with hard mast reserves (Whitaker 2003). This method requires monitoring the stand to be treated for 3

consecutive years to identify and marking individual trees that are above average acorn producers (Healy 1997). A traditional clearcut is then conducted in the stand, but marked trees are left standing. The regenerating stand eventually will provide high quality escape and drumming cover for ruffed grouse and the remaining oaks provide a high quality food resource and oak regeneration. Alternatively, clearcuts can be planned to intersperse early successional stands that are adjacent or in close proximity to acorn producing stands. In mixed-mesophytic forests, where alternative food tree species, including birch and cherry are present traditional clearcutting is recommended (Whitaker 2003).

Access routes, including roads, skid roads, landings, and trails appear to be important alternative feeding sites for ruffed grouse in oak-hickory forests (Whitaker 2003). In springs following poor acorn production, ruffed grouse increased selection for roads presumably due the availability of alternative food resources (Whitaker 2003). We recommend seeding roads and clearings with a mixture of native legumes and grasses to provide feeding sites for grouse broods (Haulton 1999) and alternative food resources for adult grouse in years following poor acorn production (Whitaker 2003)

Nesting cover - In the Great Lakes region early-successional forest stands provide most, if not all, habitat requirements for ruffed grouse. In New York most grouse established nests in early-succession stands with little understory cover, but considerable amounts of summer food for broods (Bump et al. 1947). Less than a third of grouse established nests in mature forest stands (Bump et al. 1947). In contrast, ruffed grouse nesting cover in the southern and central Appalachians consists of mid-age to mature, pole-sized (12.5-27.8 cm dbh) stands with an understory consisting of

21-60% coarse-woody debris and <30% herbaceous vegetation (Tirpak and Giuliano 2004). In the southern and central Appalachians nesting cover can be created using group selection cuts in pole and sawtimber stands to reduce basal area, open the mid-story canopy, and increase herbaceous ground cover (Tirpak and Giuliano 2004). Additionally, small canopy gaps (0.4-2 ha) can be created by girdling trees. The added benefit of this method is that, over time, it will increase the amount of coarse woody debris on the ground which is an important characteristic of ruffed grouse nesting cover.

Brood cover - Mortality rates of ruffed grouse chicks in the southern and central Appalachian region are highest in the first week post-hatch (Haulton 1999, Smith et al. 2004) as females move their brood from the nest to brood cover. Young stands with sparse crown canopy and complex ground cover (Bump et al. 1947) provide the necessary resources for grouse broods throughout most of grouse range. In the southern and central Appalachian region brood cover (to 6-weeks post-hatch) is characterized by open mid-age or mature forests stands with tall, complete, vegetative ground cover, and pockets of rhododendron or mountain laurel (Haulton 1999). Broods are also commonly found in mesic bottomlands, presumably due to the higher abundance of herbaceous ground cover and associated arthropod abundance. High quality brood cover can be created through group selection or thinning operations in mid-age forest stands followed by prescribed burning to maintain an open mid-story and facilitate growth of herbaceous ground cover (Haulton 1999). Management activities located on mesic soils will presumably result in increased abundance of herbaceous cover and arthropods (Haulton 1999, Whitaker 2003).

Interspersion of cover types - In the Appalachian region, ruffed grouse make daily migrations between ridge tops and mesic bottomlands to obtain necessary resources (Whitaker 2003) and females with newly hatched chicks leave the nest site within 24-hours of hatching to locate brood cover. Daily and seasonal changes in habitat requirements and movement patterns suggest that the interspersion of early-successional forest patches (2-16ha) that provide a diversity of cover types (e.g., escape, foraging, nesting, and brood cover) is a critical aspect of successful habitat management for ruffed grouse in the Appalachian region (Fearer 1999, Whitaker 2003). Due to the diversity of cover types used on an annual basis and daily movement patterns we recommend land managers use a variety of silvicultural practices including clearcutting, clearcutting with hard mast reserves, group selection cuts, girdling, and prescribed fire to create a mosaic of stand ages, and stand structure (i.e., size and shape) across the landscape. Interspersion of cover types and habitat requirements should reduce home range size and movement, thus decrease predation risk and energy expenditure by individual grouse and possibly result in increased productivity. Additionally, we believe interspersion of nesting and brood cover will decrease distances moved by broods, particularly in the first 7 days post-hatch and has the potential to increase chick survival.

Hunting – Our results indicate adult ruffed grouse in the Appalachian region experience high survival rates and that current harvest rates (<30%) are sustainable. Yet, other research has indicated that disturbance from hunting (and other sources) including vehicle traffic and flushing can cause changes in animal behavior, physiology, habitat selection, and potentially population dynamics (Knight and Cole 1995).

Research conducted as part of the ACGRP indicated ruffed grouse have larger home ranges and make less use of preferred habitat features including regenerating clearcuts and mesic bottomlands on areas open to hunting than on areas closed to hunting (Whitaker 2003). Our results also indicate ruffed grouse in the region have lower productivity and may be nutritionally stressed, particularly during late-winter (February – March) which coincides with the late hunting season (February).

In light of these findings, we recommend state agencies manage ruffed grouse hunting in the Appalachian region at current harvest levels and for high quality experiences. We stress that managers should not strive to increase harvest rates beyond those experienced in this study because increased harvest mortality may be additive. To provide high quality hunting opportunities (i.e., low hunting pressure, low vehicle traffic, high flush rates) we recommend using road closures in conjunction with habitat management (see above). Specifically, working from the habitat recommendations of Whitaker (2003), we recommend ruffed grouse management units be divided into “refuge” and “recreational” areas. Refuge areas will minimize recreational disturbance on ruffed grouse during critical times of the year (i.e., late-winter and spring) allowing them to reduce their home range size and make more use of preferred habitat features (e.g., regenerating clearcuts, access routes, and mesic bottoms, Whitaker 2004). It is possible, though beyond the scope of our data to conclude, that refuge areas will produce birds that will disperse across the landscape and may be available to hunters in recreational areas.

Hunting pressure, harvest rates, hunter success, and thus, hunting-related disturbance are related to distance from roads or initial starting point (e.g., gate or

hunting cabin; Fischer and Keith 1974, Gullion and Alm 1983, Broseth and Pedersen 2000, Gratson and Whitman 2000, Hayes et al. 2002, McCorquodale et al. 2003). In Alberta, harvest rate (48%) was higher for birds trapped <101 m from a road than birds trapped >101 m from the road (19%; Fischer and Keith 1974). Furthermore, male grouse holding territories >201 m from the road had higher annual survival (36%) than male grouse defending territories <201 m from the road (23%; Fischer and Keith 1974). In Maine, Michigan, and Wisconsin the majority of ruffed grouse hunting occurs within 402 m of roads (Gullion and Alm 1983). In Norway, harvested willow ptarmigan lived closer to hunting cabins and had up to twice the amount of hunting pressure in their home ranges than individuals that survived the hunting season (Broseth and Pedersen 2000).

We define refuges as areas receiving habitat management treatments (i.e., timber harvest, prescribed burning, girdling, road seeding) located >402 m from any open road (Figs. 17 & 18). Recreational areas are defined as any area <402 m from an open road (Figs 17 & 18). Note, we are not recommending locating all silvicultural prescriptions >402 m from gates. In fact, to provide high quality hunting opportunities some portion of silvicultural treatments should be <402 m from gates to allow foot access. We suspect hunters will make heavy use of roads (Broseth and Pedersen 2000) and recommend placing greater emphasis on locating girdled patches along (open and seeded) roads to provide additional hunting opportunities. This type of configuration will provide high quality habitat across the entire landscape, but will also minimize disturbance in some portion while providing high quality hunting in the remaining landscape. At this time we cannot make explicit recommendations as to what

portion of the landscape or management unit should be maintained as “refuge” or “recreational” areas, but encourage implementing our recommendations in an adaptive management framework based on local management goals. An adaptive management framework will allow managers to experiment with different spatial configurations of refuge and recreational areas until successful distributions are identified.

Management of roads will require balancing sociological, ecological and economical considerations. We are not aware of any studies that have investigated attitudes towards road closures as a management tool in the Appalachian region, but studies in other areas have indicated hunters do support road closures as a management tool (Gratson and Whiteman 2000, Little 2001). In the Appalachian region, dedicated ruffed grouse hunters compose a minority of hunters (G. Norman, Virginia Department of Game and Inland Fisheries, personal communication). Many are members of the Ruffed Grouse Society and spend the majority of their time and resources in the pursuit of ruffed grouse in the Appalachian region and other parts of the United States. Their satisfaction tends to be based on time in the field, the probability of flushing grouse, and working with their dogs, not necessarily the number of harvested grouse. Other hunters will harvest ruffed grouse opportunistically, but ruffed grouse hunting is not the focus of their efforts. We suspect dedicated ruffed grouse hunters will enjoy and support road closures. In areas identified specifically for ruffed grouse management we encourage closing roads from the start of the hunting season until the end of the early-brood period (late June to mid-July). Closing roads during this period will decrease disturbance during the 2 most critical periods of the year for ruffed grouse (i.e., winter and the breeding season). In areas managed for multiple-

use, and particularly areas that experience high levels of hunting for other species, we strongly encourage closing roads in the late hunting season (i.e., mid-December) to the end of the early-brood period. This strategy should provide road access to hunters during archery, muzzleloader, and rifle seasons, but minimize disturbance to ruffed grouse during late-winter and the breeding season.

Management and Research needs – Our results have highlighted several areas that we feel require further investigation or management to improve ruffed grouse conservation in the southern and central Appalachian region. First, we believe increasing our understanding of ruffed grouse productivity and recruitment should be a priority. We believe additional research should be conducted to improve our understanding of the relationship between hard mast production and productivity (i.e., nest rate, nest success, clutch, etc.) and recruitment (to 35-days post-hatch and to brood break-up). We believe this issue could be addressed through a combination of long-term monitoring and manipulative field experiments. We also recommend additional research to obtain estimates of survival from 35-days post-hatch to brood break up (≈ 84 days-post-hatch). Second, we believe additional research is needed to determine when harvest mortality becomes additive. We suggest manipulative field studies with specified treatments of 0%, 25%, 50%, and 75% harvest rates. Assuming a field experiment could be implemented with enough samples and controlled harvest rates applied, this type of study would provide detailed information on the functional relationship between harvest mortality and survival. Third, we feel there is a need for population-level genetics research to test our hypothesis that ruffed grouse in the southern and central Appalachian region exhibit clinal population structure. Genetic

research could provide insight into the genetic structure of ruffed grouse populations in the Appalachian region. Genetic research may also be useful in the study of dispersal. Finally, we feel there is a great need for the development of region-wide standardized, annual indices of ruffed grouse population size and fall age ratios. We recommend conducting periodic (3-5 years) studies to obtain independent estimates of population size and age ratios. Independent estimates and indices could then be used to develop more reliable, predictive population models that could aid in ruffed grouse management.

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Table 1. Description of study sites participating in the Appalachian Cooperative Grouse Research Project, 1996-2002.

Study Area	Ownership	Counties	RPI ^a	Forest Type ^b	Treatment ^c	Years
KY1	State	Lawrence	8.21	Oak-Hickory	Closed	1996-2002
MD1	State	Garrett	33.62	Mixed-Mesophytic	Open	1996-2002
NC1	Federal	Macon	32.4	Mixed-Mesophytic	N/A	1999-2002
OH1	State, Private	Athens, Vinton, Meigs	N/A	N/A	N/A	1996-1999
OH2	State, Private	Coshocton	N/A	N/A	N/A	1996-1999
PA1	State	Clearfield, Elk	35.96	Mixed-Mesophytic	N/A	1998-2002
RI1	State	Kent	25.54	Oak-Hickory	N/A	1999-2002
VA1	Federal	Augusta	25.0	Oak-Hickory	Open	1997-2002
VA2	MeadWestvaco	Botetourt	27.81	Oak-Hickory	Open	1996-2002
VA3	State	Smyth, Washington	33.13	Mixed-Mesophytic	Closed	1996-2002
WV1	MeadWestvaco	Randolph	34.73	Mixed-Mesophytic	Open	1996-2002
WV2	MeadWestvaco	Greenbrier	28.15	Oak-Hickory	Closed	1996-2002

^a Relative phenological index (RPI) estimates timing of phenological events based on latitude, longitude, and elevation following Hopkins bioclimatic rule (1938). Higher values indicate later timing of phenological events.

^b Study areas were classified as mixed-mesophytic or oak-hickory forest associations based on tree species composition (J. Tirpak, unpublished data), literature review (Braun 1950), and RPI.

^c Seven study areas were used in the experimental test of the compensatory mortality hypothesis. Closed sites were open for normal ruffed grouse hunting seasons during fall 1996 – 1998 and closed to ruffed grouse hunting during fall 1999 – 2001. Open sites served as controls and remained open to normal ruffed grouse hunting seasons throughout the study (1996 – 2002).

Table 2. Ruffed grouse reproductive parameters estimated as part of the Appalachian Cooperative Grouse Research Project, 1997-2002.

Parameter	Description
Nesting rate (NR)	The proportion of hens that were considered to have attempted to nest as determined by radio telemetry locations (Vangilder 1992, Vangilder and kurzejeski 1995).
Incubation Date (INCD)	Estimated by back dating from hatch date assuming a 24-day incubation period.
Mean clutch size (Clutch)	Determined by flushing nesting hens during the 2 nd or 3 rd week of incubation and counting all visible eggs. Includes clutches of hens killed during the incubation period.
Nest success (NS)	The proportion of nests from which ≥ 1 chick hatched. Includes nests of hens killed during the incubation period (Roberts et al. 1995).
Re-nesting rate (RNR)	The proportion of hens with failed 1 st nest attempts that were considered to have made a 2 nd nesting attempt (Vangilder and Kurzejeski 1995).
Hatchability (HATCH)	The proportion of eggs from successful 1 st nests that ultimately hatched (Vangilder and Kurzejeski 1995).
Hen Success (HS)	The proportion of hens alive on 1 April that hatch ≥ 1 chick from a 1 st or 2 nd nest.
35-day chick survival (S ₃₅)	The proportion of chicks in a brood alive at 35-days post-hatch, including broods of hens killed prior to 35-days post-hatch.

Table 3. Predictor variables used to develop *a-priori* models of factors affecting ruffed grouse reproductive ecology in the southern and central Appalachian region, 1997-2002.

VARIABLE	DESCRIPTION
Study Area (SA)	Dummy variable to indicate study area
Year	Dummy variable to indicate year of the investigation (i.e., 0-5)
Age	Dummy variable to indicate the age of the female as either juvenile (first breeding season) or adult. Juveniles were graduated to adults each year.
Mast	An evaluation of the mast crop production in the fall [$Y = 7.96 + 6.92(\text{Chestnut Oak Score})$; Devers et al. unpublished data].
DP10	The number of days with ≥ 1 inch precipitation (NOAA data) in specified month or season.
DPNT	Departure from normal monthly temperature (NOAA data) in specified month or season.
MMNT	Monthly mean minimum temperature (NOAA data) in specified month or season.
TPCP	Total precipitation (NOAA data) in specified month or season.
Month	Temperature and precipitation data used for specific months specified in the model.
Forest	A classification of each site as either oak-hickory or mixed mesophytic forest association.

Table 4. Predictor variables used to develop *a-priori* models of ruffed grouse survival during a 5-year period (1997 – 2002) in the southern and central Appalachian region, 1997-2002.

VARIABLE	DESCRIPTION
Study Area (SA)	Dummy variable to indicate study site
Time	Seasonal time step included: spring (Apr – Jun), summer (Jul – Sep), fall (Oct – Dec), and winter (Jan – Mar).
Age	Dummy variable to indicate the age of the individual as either juvenile (hatch year) or adult (after hatch year) at time of capture.
Sex	Dummy variable to indicate the gender of the individual as male or female.
Mass	The mass of an individual at time of capture.
Mast	An index of mast crop production the previous fall [$Y = 7.96 + 6.92(\text{Chestnut Oak Score})$; Devers et al. unpublished data].
Forest	Classifications of each study site as either oak-hickory or mixed mesophytic forest type.

Table 5. Description of variables used in the development of *a-priori* models in the investigation of ruffed grouse annual and seasonal survival in the southern and central Appalachian region, 1997 – 2002.

VARIABLE	DESCRIPTION
Study Area (SA)	Dummy variable to indicate study site
Time ¹	Annual survival analysis used a seasonal time step including spring (Apr – Jun), summer (Jul – Sep), fall (Oct – Dec), and winter (Jan – Mar). Monthly times step was used for seasonal survival analyses.
Age	Dummy variable to indicate the age of the individual as either juvenile (hatch year) or adult (after hatch year). Individuals were graduated on 1 July.
Sex	Dummy variable to indicate the gender of the individual as male or female.
Mast	An index of the mast crop production the previous fall based on the mast index of $[Y = 7.96 + 6.92(\text{Chestnut Oak Score})]$; Devers et al. unpublished data].
Forest	Classifications of each site as either oak-hickory or mixed mesophytic forest association.
PREY	The average number of rabbits (<i>Sylvilagus floridanus</i>) and squirrels (<i>Sciurus caolinensis</i>) observed per hour by month or season.
RAPTOR	The average number of Cooper's hawks (<i>Accipiter cooperii</i>) and owls (<i>Strix</i> spp.) observed per hour averaged by season.
MMNT	Mean minimum monthly temperature averaged by month or season.
PPT	The total precipitation per month averaged by season.
SNOW	The mean number of days with crusted snow during winter.

¹ Monthly time step used for seasonal survival analyses.

Table 6. Summary of ruffed grouse vital rates at 3 spatial scales in the southern and central Appalachian region, 1996 – 2002 used in the development of a stochastic population projection model. Estimates at the regional level (the Appalachian region) and forest level (e.g., oak-hickory [OH] or mixed-mesophytic [MM]) were pooled across sites and averaged across years. Mean estimates at the site level were averaged across sites and years.

Scale									
Parameter	Distrib.	Regional			Forest			Site	
		<i>n</i>	Bounds		OH	MM	OH	MM	
Nest Rate (E)	Uniform	6	0.87 – 1.0	6	0.75 – 1.0	6	0.94 – 1.0	26	0.1 – 1.0
Nest Success (G)	Uniform	6	0.61 – 0.74	6	0.52 – 0.82	6	0.63 – 0.81	24	0.17 – 1.0
Clutch (C)	Normal	6	9.67 ± 0.565 sd	6	9.15 ± 0.698 sd	6	10.01 ± 0.681 sd	24	9.10 ± 1.383 sd
Hatchability (H)	Uniform	6	0.87 – 1.0	6	0.76 – 1.0	6	0.86 – 1.0	24	0.67 – 1.0
Re-Nest Rate (I)	Uniform	6	0.0 – 0.5	6	0.0 – 0.3	6	0.0 – 0.5	15	0.0 – 1.0
2 nd Nest Success (J)	Uniform	6	0.33 – 0.77	6	0.33 – 0.77 ^a	6	0.33 – 0.77 ^a	6	0.33 – 0.77 ^a
2 nd Clutch Size (K)	Uniform	6	7.0 ± 1.686 sd	6	7.0 ± 1.686 sd ^a	6	7.0 ± 1.686 sd ^a	6	7.0 ± 1.686 sd ^a

^a Used estimates of mean and standard deviation from regional scale due to the lack of observations among years and sites at the site-level scale.

^b Estimates of survival rates were calculated on the log normal scale using Program Mark.

Table 6. Continued.

Scale													
Forest													
Site													

^a Used estimates of mean and standard deviation from regional scale due to the lack of observations among years and sites at the site-level scale.^b Estimates of survival rates were calculated on the log normal scale using Program Mark.

Table 7. Parameters used in the development of deterministic (1 and 2) and a stochastic (S) ruffed grouse population models. Demographic bounds for each variable and spatial scale are reported in Table 6.

Parameter	Models	Distribution	Description
Nest Rate (E)	1	Uniform	The proportion of hens alive on 1 April that attempt to nest.
Nest Success (G)	1	Uniform	The proportion of hens that attempt to nest that hatch ≥ 1 chick.
Clutch (C)	1	Normal	The number of eggs laid.
Hatchability (H)	1	Uniform	The proportion of eggs in a clutch that hatch.
Re-Nest Rate (I)	1	Uniform	The proportion of hens with failed first nest attempts that attempt to lay a second clutch.
2 nd Nest Success (J)	1	Uniform	The proportion of hens that attempt a second nest that hatch ≥ 1 chick.
2 nd Clutch Size (K)	1	Normal	The number of eggs laid in a second nest attempt.
2 nd Hatchability (L)	1	Uniform	The proportion of eggs in a second clutch that hatch

Table 7. Continued.

Parameter	Models	Distribution	Description
Chick Survival (B)	1	N/A.	The probability of a chick surviving to 35-days post-hatch as a function of mast production the previous fall ($B = 0.132 + 0.007 \cdot M$)
Chick Production (F')	2, S	Normal	The number of chicks age 35-days post-hatch per female alive on 1 April as a function of mast production the previous fall ($F' = 1.16 + 0.052 \cdot M$).
Spring Survival (p)	1, 2, S	Normal	The probability of an adult grouse surviving the spring season.
Summer Survival (s)	1, 2, S	Normal	The probability of an adult grouse surviving the summer season.
Fall Survival (f)	1, 2, S	Normal	The probability of an adult grouse surviving the fall season.
Winter Survival (w)	1, 2, S	Normal	The probability of an adult grouse surviving the winter season.
Mast Index (M)	1, 2, S	Uniform	An index of hard mast production in the fall [$Y = 7.96 + 6.92(\text{Chestnut Oak Score})$]; Devers et al. unpublished data].

Table 8. Summary of ruffed grouse fall trap success in the southern and central Appalachian region by study site, 1996 – 2002. Sample size (n) refers to the number of years.

Study Area	Grouse/100 Trap nights				Flushes/100 Trap nights ^a			
	n	\bar{x}	se	95% CI	n	\bar{x}	se	95% CI
KY1	6	1.41	0.314	0.60 – 2.21	6	0.60	0.215	0.05 – 1.15
MD1	5	2.17	0.482	0.83 – 3.51	5	1.81	0.454	0.55 – 3.07
NC1	3	0.89	0.135	0.31 – 1.47
OH1	1	3.2	.	.	1	1.03	.	.
OH2	2	4.59	0.930	0.0 – 16.41	2	1.66	1.050	0.0 – 15.00
PA1	4	6.00	1.23	2.06 – 9.92	4	1.98	0.201	1.34 – 2.62
RI1	3	1.23	0.289	0.0 – 2.48	3	0.51	0.182	0.0 – 1.29
VA1	5	0.87	0.168	0.41 – 1.34	5	2.22	0.384	1.16 – 3.29
VA2	6	1.06	0.322	0.23 – 1.88	6	1.27	0.236	0.66 – 1.88
VA3	6	1.13	0.065	0.96 – 1.29	6	0.35	0.087	0.13 – 0.58
WV1	6	3.00	0.391	2.00 – 4.00	6	2.13	0.481	0.90 – 3.37
WV2	6	4.71	0.551	3.29 – 6.13

^a Defined as the number of birds flushed from the vicinity of a trap during routine trapping activities.

Table 9. Summary of fall age ratios [juvenile (J), female (F), and adult (A)] of trapped ruffed grouse in the southern and central Appalachian region by study site, 1996 – 2001. Sample size (n) refers to the number of years.

Study Area	J:AF				JF:AF			
	n	\bar{x}	se	95% CI	n	\bar{x}	se	95% CI
KY1	6	0.53	0.127	0.21 – 0.86	6	0.30	0.084	0.09 – 0.52
MD1	6	1.31	0.592	0.0 – 2.83	6	0.70	0.345	0.0 – 1.59
NC1	3	0.53	0.174	0.0 – 1.28	3	0.32	0.115	0.0 – 0.81
OH1	3	0.45	0.164	0.0 – 1.15	3	0.27	0.120	0.0 – 0.79
OH2	4	0.36	0.110	0.02 – 0.71	4	0.19	0.058	0.00 – 0.37
PA1	4	0.74	0.137	0.31 – 1.18	4	0.38	0.069	0.16 – 0.60
RI1	3	0.47	0.168	0.0 – 1.19	3	0.18	0.111	0.0 – 0.66
VA1	5	1.03	0.336	0.10 – 1.97	5	0.44	0.197	0.0 – 0.99
VA2	6	0.24	0.074	0.05 – 0.43	6	0.13	0.044	0.02 – 0.24
VA3	6	0.28	0.064	0.11 – 0.44	6	0.17	0.030	0.09 – 0.24
WV1	6	0.32	0.074	0.12 – 0.51	6	0.12	0.039	0.02 – 0.22
WV2	6	0.42	0.104	0.15 – 0.68	6	0.15	0.052	0.02 – 0.29

Table 10. Summary of ruffed grouse reproductive rates in the southern and central Appalachian region, 1997-2002 (pooled across sites and years).

Parameter	n	\bar{x}	se	95% CI
Nesting Rate	437	0.96	0.001	0.94-0.98
Incubation Date	351	1 May	0.421	30 April – 2 May
Clutch Size	368	9.86	0.111	9.64-10.07
Hatchability ^a	384	0.82	.	.
Nest Success	410	0.66	0.023	0.62-0.71
Re-nest Rate	111	0.23	0.040	0.16-0.31
Hen Success	411	0.68	0.023	0.64-0.73
35-day Chick Survival	235	0.22	0.016	0.19-0.25

^a We report median hatchability due to skewness of the data.

Table 11. *A-priori* models and results of information theoretic model selection process of ruffed grouse nesting rate in the southern and central Appalachian region, 1997-2002 (n = 279). Models were fit using logistic regression.

Model	Description	K	Log L	AIC _c	Δ_i	ω_i	Conc. ^a	Discor. ^b	Tied ^c
19	NR = β_0 + Forest + YR + ϵ	7	-45.568	105.55	0.00	0.70	84.9	8.7	6.4
18	NR = β_0 + Forest + ϵ	2	-52.577	109.20	3.65	0.11	56.3	0.0	43.7
23	NR = β_0 + Age + Forest + YR + ϵ	4	-51.403	110.95	5.40	0.05	81.5	14.9	3.6
20	NR = β_0 + Age + Forest + ϵ	3	-52.559	111.21	5.66	0.04	67.3	10.0	22.7
25	NR = β_0 + Forest + Mast + ϵ	3	-52.576	111.24	5.69	0.04	72.1	12.2	15.8
22	NR = β_0 + Age + Forest + YR + DP10 _(MAR) + (DP10 _(MAR) *DP10 _(MAR)) + ϵ	6	-50.282	112.87	7.32	0.02	81.6	16.0	2.3
21	NR = β_0 + Age + Forest + (Age*Forest) + ϵ	4	-52.559	113.26	7.71	0.01	67.3	10.0	22.7
28	NR = β_0 + Forest + Mast + (Forest*Mast) + ϵ	4	-52.576	113.30	7.75	0.01	72.1	12.2	15.8
26	NR = β_0 + Forest + Age + Mast + DP10 _(MAR) + DP10 _(MAR) ²	6	-51.279	114.87	9.32	0.01	81.1	16.4	2.5
27	NR = β_0 + Age + Forest + DP10 _(MAR) + DP10 _(MAR) ² + ϵ	6	-51.332	114.97	9.42	0.01	78.3	14.8	6.8
3	NR = β_0 + YR + ϵ	6	-56.753	125.81	20.27	0.00	71.6	14.9	13.5

^a Concordance

^b Discordance

Table 11. Continued

Model	Description	K	Log L	AIC _c	Δ_i	ω_i	Conc. ^a	Discor. ^b	Tied
5	NR = $\beta_0 + \text{MMNT}_{(W_{in})} + \varepsilon$	2	-62.091	128.23	22.68	0.00	71.2	25.6	3.3
Null	NR = $\beta_0 + \varepsilon$	1	-66.742	135.50	29.95	0.0	.	.	.
6	NR = $\beta_0 + \text{DP10}_{(MAR)} + \varepsilon$	2	-66.610	137.26	31.71	0.00	39.7	38.1	22.2
1	NR = $\beta_0 + \text{Age} + \varepsilon$	2	-66.635	137.31	31.76	0.00	27.2	21.6	51.2
4	NR = $\beta_0 + \text{Mast} + \varepsilon$	2	-66.653	137.35	31.80	0.00	47.6	46.0	6.4
11	NR = $\beta_0 + \text{Age} + \text{Mast} + (\text{Age} * \text{Mast}) + \varepsilon$	4	-65.041	138.23	32.68	0.00	61.2	34.5	4.4
14	NR = $\beta_0 + \text{DP10}_{(MAR)} + \text{DP10}_{(MAR)}^2 + \varepsilon$	3	-66.492	139.07	33.52	0.00	33.1	37.7	29.3
10 ^c	NR = $\beta_0 + \text{Age} + \text{Mast} + \varepsilon$	3	-66.531	139.15	33.60	0.00	51.9	42.0	6.1
2 ^c	NR = $\beta_0 + \text{SA} + \varepsilon$	9
7 ^c	NR = $\beta_0 + \text{SA} + \text{YR} + \varepsilon$	14
8 ^c	NR = $\beta_0 + \text{SA} + \text{Age} + \varepsilon$	10
9 ^c	NR = $\beta_0 + \text{SA} + \text{Age} + (\text{SA} * \text{Age}) + \varepsilon$	17
12 ^c	NR = $\beta_0 + \text{Age} + \text{YR} + \varepsilon$	7
13 ^c	NR = $\beta_0 + \text{Age} + \text{YR} + (\text{Age} * \text{YR}) + \varepsilon$	12

^a Concordance^b Discordance^c Maximum likelihood estimate was not achieved thus parameter estimates are not reliable.

Table 11. Continued

Model	Description	K	Log L	AIC _c	Δ_i	ω_i	Conc. ^a	Discor. ^b	Tied ^c
15 ^d	NR = β_0 + SA + Age + Mast + DP10 _(Mar) + MMNT _(Win) + Mast*MMNT _(Win) + ε	14
24 ^d	NR = β_0 + Forest + SA(Forest + ε)	9
Global	NR = β_0 + SA + Age + YR + DP10 _(Mar) + DP10 _(Mar) ² + ε	17
16 ^d	NR = β_0 + SA + Age + YR + ε	15
17 ^d	NR = β_0 + Age + YR + MMNT _(Win) + (YR*MMNT _(Win) + ε)	13

^a Concordance^b Discordance^c Tied^d Maximum likelihood estimate was not achieved thus parameter estimates are not reliable.

Table 12. *A-priori* models and results of information theoretic model selection process of ruffed grouse incubation date (INCD) in the southern and central Appalachian region, 1997-2002 (n=176). Models were fit using linear regression.

Model	Description	K	RSS	Log L	AIC _c	Δ_i	ω_i	R^2	R^2_{adj}
10	INCD = β_0 + Age + SA + YR + Mast + DPNT _(win) + MMNT _(win) + (Mast*MMNT _(win)) + ϵ	16	6257.30	-314.25	663.92	0.00	0.69	0.40	0.35
35	INCD = β_0 + Forest + SA(Forest) + YR + Forest*YR + ϵ	15	6464.80	-317.12	667.24	3.32	0.13	0.38	0.33
17	INCD = β_0 + SA + Age + YR + DPNT _(win) + ϵ	10	6959.61	-323.61	668.55	4.63	0.07	0.33	0.30
19	INCD = β_0 + SA + Age + Mast + DPNT _(win) + (Mast*DPNT _(win)) + ϵ	12	6791.28	-321.46	666.91	4.91	0.06	0.35	0.31
18	INCD = β_0 + SA + Age + YR + MMNT _(win) + ϵ	13	6745.57	-320.86	669.97	6.05	0.03	0.34	0.31
20	INCD = β_0 + SA + Age + Mast + MMNT _(win) + (Mast*MMNT _(win)) + ϵ	11	6964.84	-323.68	670.96	7.04	0.02	0.33	0.30
25	INCD = β_0 + Forest + Age + YR + MMNT _(win) + ϵ	9	7371.05	-328.67	676.41	12.49	0.00	0.28	0.26
1	INCD = β_0 + SA + ϵ	7	7605.13	-331.42	677.50	13.58	0.00	0.27	0.25
30	INCD = β_0 + Forest + SA(Forest) + ϵ	7	7605.13	-331.42	677.50	13.58	0.00	0.27	0.25
28	INCD = β_0 + Forest + Age + Mast + DPNT _(win) + MAST*DPNT _(win) + ϵ	8	7553.34	-330.81	678.49	14.57	0.00	0.28	0.25
31	INCD = β_0 + Forest + SA(Forest) + ϵ	9	7482.60	-329.99	679.06	15.14	0.00	0.28	0.25
29	INCD = β_0 + Forest + Age + Mast + MMNT _(win) + MAST*MMNT _(win) + ϵ	7	7708.35	-332.60	679.21	15.95	0.00	0.26	0.24

Table 12. Continued

Model	Description	K	RSS	Log L	AIC _c	Δ_i	ω_i	R ²	R ² _{adj}
27	INCD = β_0 + Forest + Age + Mast + MMNT _(WIN) + ε	6	7903.65	-334.80	682.11	18.18	0.00	0.24	0.23
9	INCD = β_0 + SA + YR + ε	11	7426.16	-329.32	682.25	18.33	0.00	0.27	0.25
32	INCD = β_0 + Forest + SA(Forest) + YR + ε	11	7426.19	42.1943	682.25	18.33	0.00	0.27	0.25
36	INCD = β_0 + SA + Age + ε	4	8116.70	-337.15	682.52	18.60	0.00	0.22	0.21
37	INCD = β_0 + SA + Forest + ε	4	8116.70	-337.15	682.52	18.60	0.00	0.22	0.21
8	INCD = β_0 + MMNT _(APR) + ε	3	8227.50	-338.34	682.82	18.90	0.00	0.21	0.21
24	INCD = β_0 + Forest + Age + YR + DPNT _(WIN) + ε	10	7565.83	-330.96	683.25	19.33	0.00	0.26	0.24
34	INCD = β_0 + Age + Forest + Mast + ε	5	8094.08	-336.90	684.15	20.23	0.00	0.22	0.21
16	INCD = β_0 + Forest + SA(Forest) + YR + Forest*YR + ε	5	8120.25	-337.18	684.72	20.80	0.00	0.22	0.21
26	INCD = β_0 + Forest + Age + Mast + DPNT _(WIN) + ε	7	7959.84	-335.43	685.52	21.60	0.00	0.24	0.22
6	INCD = β_0 + MMNT _(WIN) + ε	3	8793.52	-344.19	694.53	30.60	0.00	0.16	0.15
21	INCD = β_0 + Forest + ε	3	8794.87	-344.21	694.55	30.63	0.00	0.16	0.15
Global	INCD = β_0 + YR + SA + (YR*SA) + ε	31	5952.32	-309.85	695.48	31.56	0.00	0.34	0.32
12	INCD = β_0 + Mast + MMNT _(WIN) + ε	4	8782.03	-344.08	696.39	32.47	0.00	0.16	0.15
33	INCD = β_0 + Forest + Mast + Forest*Mast + ε	5	8745.38	-343.71	697.77	33.85	0.00	0.16	0.15

Table 12. Continued

Model	Description	K	RSS	Log L	AIC _c	Δ_i	ω_i	R ²	R ² _{adj}
22	INCD = β_0 + Forest + YR + ε	7	8690.66	-343.16	700.98	37.06	0.00	0.16	0.14
23	INCD = β_0 + Forest + YR + Forest*YR + ε	18	7770.82	-333.31	706.98	43.06	0.00	0.22	0.22
2	INCD = β_0 + Age + ε	3	9692.73	-352.76	711.66	47.74	0.00	0.07	0.07
15	INCD = β_0 + Age + Mast + DPNT _(WIN) + ε	6	9424.57	-350.29	713.08	49.16	0.00	0.10	0.08
13	INCD = β_0 + Age + Mast + (Age*Mast) + ε	5	9600.31	-351.92	714.19	50.27	0.00	0.08	0.06
14	INCD = β_0 + Age + YR + (YR*Age) + ε	11	9230.18	-348.46	720.53	56.60	0.00	0.07	0.07
Null	INCD = β_0 + ε	1	10439.2	-359.29	722.65	58.73	0.00	0.00	0.00
4	INCD = β_0 + Mast + ε	3	10374.9	-358.75	723.63	59.17	0.00	0.01	0.00
11	INCD = β_0 + Mast + DPNT _(WIN) + ε	5	10348.6	-357.42	725.19	61.27	0.00	0.02	0.00
5	INCD = β_0 + DPNT _(WIN) + ε	4	10348.6	-358.52	725.28	61.36	0.00	0.01	0.00
7	INCD = β_0 + DPNT _(APR) + ε	4	10348.6	-358.52	725.28	61.36	0.00	0.01	0.00
3	INCD = β_0 + YR + ε	6	10200.6	-357.26	727.01	63.09	0.00	0.01	0.00

Table 13. *A-priori* models and results of information theoretic model selection process of ruffed grouse clutch size in the southern and central Appalachian region, 1997-2002 ($n = 211$). Models were fit using linear regression.

Model	Description	K	RSS	Log L	AIC _c	Δ_i	ω_i	R ²	R ² _{adj}
25	Clutch = β_0 + Forest + Mast + SA(Forest) + ϵ	8	713.61	-128.55	273.81	0.00	0.22	0.12	0.09
1	Clutch = β_0 + SA + ϵ	7	721.97	-129.78	274.11	0.30	0.19	0.11	0.08
23	Clutch = β_0 + SA + Age + Mast + ϵ	9	711.29	-128.21	275.31	1.50	0.10	0.12	0.09
28	Clutch = β_0 + Forest + Age + Mast + SA(Forest) + ϵ	9	711.29	-128.21	275.31	1.50	0.10	0.12	0.09
9	Clutch = β_0 + SA + YR + ϵ	12	690.53	-125.08	275.74	1.93	0.08	0.12	0.10
26	Clutch = β_0 + Forest + YR + SA(Forest) + ϵ	12	690.53	-125.08	275.74	1.93	0.08	0.12	0.10
30	Clutch = β_0 + Forest + Mast + SA(Forest) + Mast*Forest + ϵ	9	713.23	-128.49	275.88	2.07	0.08	0.12	0.09
29	Clutch = β_0 + Forest + Age + Mast + SA(Forest) + Mast*Forest + ϵ	10	710.65	-128.11	277.32	3.51	0.04	0.12	0.09
10	Clutch = β_0 + Forest + Mast + ϵ	4	759.01	-135.06	278.31	4.50	0.02	0.06	0.05
7	Clutch = β_0 + Forest + ϵ	3	766.64	-136.11	278.34	4.53	0.02	0.05	0.05
18	Clutch = β_0 + SA + Age + Yr + Mast + MMNT _(WIN) + (Mast*MMNT _(WIN)) + ϵ	16	670.39	-121.96	278.72	4.91	0.02	0.15	0.11
24	Clutch = β_0 + Age + Forest + Mast + ϵ	5	753.55	-134.29	278.88	5.07	0.02	0.07	0.05
27	Clutch = β_0 + Forest + Mast + Forest*Mast + ϵ	5	759.01	-135.06	280.40	6.59	0.01	0.06	0.05
15	Clutch = β_0 + Forest + Mast + (Forest*Mast) + ϵ	5	759.01	-135.06	280.40	6.59	0.01	0.06	0.05

Table 13. Continued.

Model	Description	K	RSS	Log L	AIC _c	Δ_i	ω_i	R ²	R ² _{adj}
11	Clutch = β_0 + Forest + YR + ϵ	8	739.79	-132.35	281.41	7.60	0.00	0.06	0.06
6	Clutch = β_0 + MMNT _(WIN) + ϵ	3	781.27	-138.11	282.33	8.52	0.00	0.03	0.03
13	Clutch = β_0 + Mast + MMNT _(WIN) + ϵ	4	778.20	-137.69	283.57	9.76	0.00	0.04	0.03
22	Clutch = β_0 + Age + Mast + MMNT _(WIN) + ϵ	5	774.68	-137.21	284.72	10.91	0.00	0.04	0.03
20	Clutch = β_0 + Mast + MMNT _(WIN) + (Mast*MMNT _(WIN)) + ϵ	5	777.29	-137.57	285.43	11.62	0.00	0.04	0.02
19	Clutch = β_0 + Mast + DPNT _(WIN) + (Mast2*DPNT _(WIN)) + ϵ	5	777.29	-137.57	285.43	11.62	0.00	0.04	0.02
5	Clutch = β_0 + DPNT _(WIN) + ϵ	3	799.58	-140.55	287.22	13.40	0.00	0.01	0.01
NULL	Clutch = β_0 + ϵ	2	807.98	-141.65	287.36	13.55	0.00	0.00	0.00
3	Clutch = β_0 + YR + ϵ	7	773.32	-137.03	288.60	14.79	0.00	0.02	0.02
2	Clutch = β_0 + Age + ϵ	3	805.27	-141.30	288.71	14.90	0.00	0.00	0.00
4	Clutch = β_0 + Mast + ϵ	3	806.46	-141.45	289.03	15.21	0.00	0.00	0.00
12	Clutch = β_0 + Mast + DPNT _(WIN) + ϵ	4	798.69	-140.43	289.06	15.25	0.00	0.01	0.00
8	Clutch = β_0 + Age + Mast + ϵ	4	803.31	-141.04	290.28	16.47	0.00	0.01	0.00
21	Clutch = β_0 + Age + Mast + DPNT _(WIN) + ϵ	5	795.90	-140.06	290.42	16.61	0.00	0.02	0.00
14	Clutch = β_0 + Age + Mast + (Age*Mast) + ϵ	5	802.50	-140.94	292.16	18.35	0.00	0.01	0.00
17	Clutch = β_0 + Age + YR + (Age*YR) + ϵ	13	746.54	-133.31	294.47	20.66	0.00	0.03	0.02
16	Clutch = β_0 + Forest + YR + (YR*Forest) + ϵ	21	689.83	-124.97	296.84	23.03	0.00	0.10	0.10
Global	Clutch = β_0 + SA + YR + (SA*YR) + ϵ	37	571.32	-105.09	300.43	26.62	0.00	0.17	0.15

Table 14. Results of post-hoc information theoretic model selection process of ruffed grouse clutch size in the southern and central Appalachian region, 1997-2002 (n = 186).

Model	Description	K	RSS	Log L	AIC _c	Δ_i	ω_i	R ²	R ² _{adj}
E	Clutch = β_0 + Forest + SA(Forest) + INCD + ε	8	579.67	-105.71	228.24	0.00	0.76	0.15	0.12
D	Clutch = β_0 + SA + Age + Mast + INCD + ε	10	575.15	-104.99	231.23	2.99	0.17	0.15	0.11
C	Clutch = β_0 + SA + Age + Mast + NF + ε	11	575.14	-104.98	233.49	5.24	0.06	0.15	0.11
25 ^a	Clutch = β_0 + Forest + Mast + SA(Forest) + ε	8	610.64	-110.56	237.92	9.68	0.01	0.10	0.07
1 ^a	Clutch = β_0 + SA + ε	12	590.72	-107.47	240.74	12.50	0.00	0.11	0.08
B	Clutch = β_0 + SA + Age + Mast + NF + ε	10	609.88	-110.44	242.14	13.89	0.00	0.10	0.06
A	Clutch = β_0 + SA + Age + Mast + NF + SA*NF + ε	15	581.08	-105.94	244.70	16.46	0.00	0.14	0.08

^a These were the most supported *a-priori* models (Table 13).

Table 15. *A-priori* models and results of information theoretic model selection process for ruffed grouse nest success in the southern and central Appalachian region, 1997-2002 (n = 226). Models were fit with logistic regression.

Model	Description	K	Log L	AIC _c	Δ_i	ω_i	Conc.	Discor.	Tied
16	NS = β_0 + Mast + MMNT _(MAR & APR) + (Mast*MMNT _(MAR & APR)) + ϵ	4	-139.18	286.55	0.00	0.14	57.6	36.5	5.9
1	NS = β_0 + SA + ϵ	9	-134.27	287.38	0.83	0.09	57.3	27.7	15.0
8	NS = β_0 + SA + YR + ϵ	10	-133.20	287.43	0.88	0.09	63.2	28.0	8.9
29	NS = β_0 + Forest + YR + SA(Forest) + ϵ	10	-133.31	287.65	1.10	0.08	63.0	31.2	5.8
Null	NS = β_0 + ϵ	1	-142.91	287.84	1.29	0.07	.	.	.
4	NS = β_0 + Mast + ϵ	2	-142.02	288.09	1.54	0.06	48.9	39.8	11.3
21	NS = β_0 + Forest + Mast + ϵ	3	-141.13	288.36	1.81	0.06	50.5	39.7	9.8
20	NS = β_0 + Forest + ϵ	2	-142.29	288.63	2.08	0.05	28.6	20.8	50.6
9	NS = β_0 + Mast + TPCP _(MAR & APR) + ϵ	3	-141.44	288.98	2.43	0.04	55.1	40.1	4.8
5	NS = β_0 + TPCP _(MAR & APR) + ϵ	2	-142.84	289.73	3.18	0.03	48.2	15.0	60.8
30	NS = β_0 + Forest + Mast + SA(Forest) + ϵ	11	-133.27	289.78	3.23	0.03	62.6	31.0	6.4
6	NS = β_0 + MMNT _(MAR & APR) + ϵ	2	-142.88	289.82	3.27	0.03	47.5	42.9	9.7
7	NS = β_0 + DP10 _(MAR & APR) + ϵ	2	-142.90	289.85	3.30	0.03	41.2	43.8	15.0
2	NS = β_0 + Age + ϵ	2	-142.91	289.87	3.33	0.03	24.5	2403.0	51.3
23	NS = β_0 + Forest + Mast + Forest*Mast + ϵ	4	-140.90	289.99	3.44	0.03	49.8	40.5	9.8
11	NS = β_0 + Mast + DP10 _(MAR & APR) + ϵ	3	-141.95	290.01	3.47	0.02	54.1	41.0	4.9

Table 15. Continued

Model	Description	K	Log L	AIC _c	Δ_i	ω_i	Conc.	Discor.	Tied
10	$NS = \beta_0 + Mast + MMNT_{(MAR \& APR)} + \epsilon$	3	-141.99	290.10	3.55	0.02	53.4	42.1	4.5
17	$NS = \beta_0 + Mast + DP10_{(MAR \& APR)} + (Mast*DP10_{(MAR \& APR)}) + \epsilon$	4	-140.96	290.11	3.56	0.02	53.7	40.1	6.3
15	$NS = \beta_0 + Mast + TPCP_{(MAR \& APR)} + (Mast*TPCP_{(MAR \& APR)}) + \epsilon$	4	-141.43	291.05	4.50	0.01	54.7	40.6	4.7
28	$NS = \beta_0 + Forest + SA(Forest)$	13	-131.73	291.17	4.63	0.01	65.0	30.4	4.6
12	$NS = \beta_0 + TPCP_{(MAR \& APR)} + MMNT_{(MAR \& APR)}$	3	-142.81	291.73	5.18	0.01	46.0	45.5	8.5
13	$NS = \beta_0 + MMNT_{(MAR \& APR)} + DP10_{(MAR \& APR)}$	3	-142.88	291.87	5.32	0.01	46.2	42.5	11.3
19	$NS = \beta_0 + MMNT_{(MAR \& APR)} + DP10_{(MAR \& APR)} + (MMNT_{(MAR \& APR)} * DP10_{(MAR \& APR)})$	4	-142.08	292.33	5.78	0.01	49.5	45.6	4.8
3	$NS = \beta_0 + YR$	5	-141.14	292.54	6.00	0.01	44.9	30.9	24.2
18	$NS = \beta_0 + TPCP_{(MAR \& APR)} + MMNT_{(MAR \& APR)} + (TPCP_{(MAR \& APR)} * MMNT_{(MAR \& APR)})$	4	-142.61	293.40	6.85	0.00	47.8	44.8	7.4
22	$NS = \beta_0 + Forest + YR$	6	-140.57	293.52	6.97	0.00	51.3	36.0	12.8
24	$NS = \beta_0 + Forest + YR + Forest*YR$	10	-137.06	295.13	8.59	0.00	48.2	23.1	28.7
25	$NS = \beta_0 + Forest + Age + MMNT_{(MAR \& APR)}$	8	-140.57	297.80	11.25	0.00	54.2	39.5	6.3

Table 15. Continued

Model	Description	K	Log L	AIC _c	Δ_i	ω_i	Conc.	Discor.	Tied
27	NS = β_0 + Forest + Age + DP10 _(MAR & APR) + (DP10 _(MAR & APR) *DP10 _(MAR & APR))	9	-140.06	298.96	12.42	0.00	57.1	38.1	4.8
26	NS = β_0 + Forest + Age + TPCP _(MAR & APR) + (TPCP _(MAR & APR) *TPCP _(MAR & APR))	9	-140.19	299.22	12.67	0.00	57.1	39.8	3.1
14	NS = β_0 + SA + Age + YR + Mast + TPCP _(MAR & APR) + MMNT _(MAR & APR) + (Mast*MMNT _(MAR & APR))	20	-129.26	302.62	16.07	0.00	68.3	29.5	2.2
Global	NS = β_0 + SA + YR + (SA*YR)	31	-119.89	312.01	25.46	0.00	71.7	22.4	5.9

Table 16. *A-priori* models and results of information theoretic model selection process for ruffed grouse re-nest rate in the southern and central Appalachian region, 1997-2002, ($n = 64$).

Model	Description	K	Log L	QAIC _c	Δ_i	ϕ_i	Conc. ^a	Discor. ^b	Tied
23	RNR = β_0 + Forest	3	-27.155	60.71	0.00	0.341	58.6	2.3	39.1
6	RNR = β_0 + MMNT _(WIN)	3	-27.472	61.34	0.63	0.249	76.8	19.5	3.6
9	RNR = β_0 + Forest + Mast	4	-26.927	62.53	1.82	0.137	77.3	14.3	8.3
11	RNR = β_0 + Mast + MMNT _(WIN)	4	-27.403	63.48	2.77	0.085	76	19.3	4.7
14	RNR = β_0 + Forest + Age + Mast	5	-26.531	64.10	3.39	0.063	79.9	15.4	4.7
22	RNR = β_0 + Forest + Age + Mast + MMNT _(WIN) + (Mast*MMNT _(WIN))	7	-24.583	65.17	4.46	0.037	85.9	12.2	1.8
18	RNR = β_0 + Forest + Age + YR	5	-27.283	65.60	4.89	0.030	77.1	19.3	3.6
1	RNR = β_0 + SA	7	-25.480	66.96	6.25	0.015	76.7	10.3	13
26	RNR = β_0 + Forest + MAST + Forest*MAST	6	-26.784	67.04	6.33	0.014	81.4	14.1	4.6
21	RNR = β_0 + Forest + Age + Mast + DPNT _(WIN) + (Mast*DPNT _(WIN))	7	-25.980	67.96	7.25	0.009	80.3	17.1	2.6
15	RNR = β_0 + SA + Age + YR + Mast + MMNT _(WIN) + (Mast*MMNT _(WIN))	9	-23.606	68.55	7.84	0.007	87.1	11.1	1.8
24	RNR = β_0 + Forest + Mast + SA(Forest)	8	-25.479	69.58	8.87	0.004	76.7	10.3	13
8	RNR = β_0 + Forest + YR	8	-25.536	69.69	8.98	0.004	78.8	11.5	9.8
16	RNR = β_0 + Forest + Age + YR	9	-24.346	70.03	9.32	0.003	84.1	10.5	5.3

^a Concordance ^b Discordance

Table16. Continued.

Model	Description	K	Log L	QAIC _c	Δ_i	ω_i	Conc. ^a	Discor. ^b	Tied
25	RNR = β_0 + Forest + Mast + SA(Forest) + MAST*Forest	9	-25.355	72.04	11.33	0.001	80.5	13.3	6.3
19	RNR = β_0 + SA + Age + Mast + DPNT _(WIN) + (Mast*DPNT _(WIN))	11	-23.831	74.74	14.03	0.000	85.2	12.9	2
20	RNR = β_0 + SA + Age + Mast + MMNT _(WIN) + (Mast*MMNT _(WIN))	11	-24.157	75.39	14.68	0.000	85.4	12.2	2.3
NULL	RNR = β_0	2	-35.989	76.18	15.47	0.000	.	.	.
2	RNR = β_0 + Age	3	-35.822	78.04	17.33	0.000	29.3	21	49.7
5	RNR = β_0 + DPNT _(WIN)	3	-35.926	78.25	17.54	0.000	49.3	42.8	7.8
7	RNR = β_0 + SA + YR	12	-24.073	78.26	17.55	0.000	84.4	12	3.6
4	RNR = β_0 + Mast	3	-35.967	78.33	17.62	0.000	47	38.8	14.2
Global	RNR = β_0 + SA + Age + YR	13	-22.625	78.53	17.82	0.000	87.4	10.8	1.8
12	RNR = β_0 + Age + Mast	4	-35.817	80.31	19.60	0.000	50.4	40.2	9.4
10	RNR = β_0 + Mast + DPNT _(WIN)	4	-35.913	80.50	19.79	0.000	47.4	46	6.6
17	RNR = β_0 + Mast + DPNT _(WIN) + (Mast*DPNT _(WIN))	5	-35.583	82.20	21.49	0.000	58.9	35.9	5.2
13	RNR = β_0 + Age + Mast + (Age*Mast)	5	-35.592	82.22	21.51	0.000	55.3	37	7.7
3	RNR = β_0 + YR	7	-33.254	82.51	21.80	0.000	48.3	19.5	32.2

^a. Concordance^b. Discordance

Table 17. *A-priori* models and results of information theoretic model selection process of ruffed grouse hen success in the southern and central Appalachian region, 1997-2002, ($n = 230$). Models were fit with logistic regression.

Model	Description	K	Log L	AIC _c	Δ_i	ω_i	Conc. ^a	Discor. ^b	Tied
28	HS = β_0 + Forest + Mast + Forest*Mast + ϵ	3	-136.56	279.22	0.00	0.24	57.2	33.9	8.9
26	HS = β_0 + Forest + Mast+ ϵ	3	-136.59	279.29	0.07	0.23	56.7	34	9.4
24	HS = β_0 + Forest+ ϵ	2	-138.06	280.17	0.95	0.15	34.8	16.6	48.6
19	HS = β_0 + Forest + Age + Mast+ ϵ	4	-136.56	281.30	2.08	0.08	59.5	35.8	4.7
15	HS = β_0 + Mast + MMNT _(MAR & APR) + (Mast*MMNT _(MAR & APR)) + ϵ	4	-137.15	282.48	3.25	0.05	59	35.7	5.3
17	HS = β_0 + Mast + TPCP _(APR & MAY)	4	-137.49	283.16	3.93	0.03	60.5	34.1	5.4
5	(Mast*TPCP _(APR & MAY)) + ϵ HS = β_0 + MMNT _(MAR & APR)	2	-139.94	283.94	4.72	0.02	55.8	40	4.2
27	HS = β_0 + Forest + YR + Forest*YR+ ϵ	10	-131.52	284.04	4.82	0.02	60.7	27.4	11.9
6	HS = β_0 + DP10 _(APR & MAY) + ϵ	2	-140.03	284.10	4.88	0.02	50.4	38.5	11.2
10	HS = β_0 + Mast + MMNT _(MAR & APR) + ϵ	3	-139.28	284.66	5.44	0.02	55.4	39.5	5
NULL	HS = β_0 + ϵ	1	-141.34	284.69	5.47	0.02	.	.	.
4	HS = β_0 + Mast+ ϵ	2	-140.53	285.11	5.89	0.01	49.8	39.8	10.4
22	HS = β_0 + Forest + YR + Age + TPCP _(APR & MAY) + MMNT _(MAR & APR) + (TPCP _(APR & MAY))* TPCP _(APR & MAY)) + ϵ	7	-135.31	285.13	5.91	0.01	49.8	39.8	10.4

^a Concordance

^b Discordance

Table 17. Continued.

Model	Description	K	Log L	AIC _c	Δ_i	ω_i	Conc. ^a	Discor. ^b	Tied
16	HS = β_0 + Mast + DP10 _(APR & MAY) + (Mast*DP10 _(APR & MAY)) + ϵ	4	-138.61	285.41	6.18	0.01	51.8	42.6	5.6
25	HS = β_0 + Forest + YR + ϵ	6	-136.58	285.54	6.31	0.01	55.4	32.8	11.8
30	HS = β_0 + Forest + SA(Forest) + MAST + ϵ	10	-132.32	285.65	6.43	0.01	64.1	30.9	4.9
11	HS = β_0 + Mast + DP10 _(APR & MAY) + ϵ	3	-139.86	285.82	6.60	0.01	54.3	40.5	5.2
12	HS = β_0 + Mast + TPCP _(APR & MAY) + ϵ	3	-139.89	285.89	6.67	0.01	55.9	39.6	4.5
7	HS = β_0 + TPCP _(APR & MAY) + ϵ	2	-141.13	286.31	7.09	0.01	48.7	45.7	5.5
2	HS = β_0 + Age + ϵ	2	-141.27	286.60	7.38	0.01	25.5	23	51.5
1	HS = β_0 + SA + ϵ	9	-134.11	287.03	7.81	0.00	57.6	28	14.4
29	HS = β_0 + Forest + SA(Forest) + ϵ	9	-134.11	287.03	7.81	0.00	57.6	28	14.4
9	HS = β_0 + Age + Mast + ϵ	3	-140.49	287.10	7.87	0.00	51.9	42.6	5.5
23	HS = β_0 + Forest + YR + Age + DP10 _(APR & MAY) + MMNT _(MAR & APR) + (DP10 _(APR & MAY)) [*]	7	-136.39	287.29	8.07	0.00	61	36.6	2.3
	DP10 _(APR & MAY) + ϵ								
31	HS = β_0 + Forest + SA(Forest) + Mast + Mast*Forest + ϵ	11	-132.22	287.65	8.43	0.00	64.5	31.1	4.4
3	HS = β_0 + YR + ϵ	5	-139.20	288.67	9.45	0.00	46	30.1	24

^a Concordance^b Discordance

Table 17. Continued.

Model	Description	K	Log L	AIC _c	Δ_i	ω_i	Conc. ^a	Discor. ^b	Tied
8	HS = β_0 + SA + YR + ϵ	10	-133.84	288.68	9.46	0.00	63.3	32.6	4.1
14	HS = β_0 + Age + Mast + (Age*Mast) + ϵ	4	-140.49	289.15	9.93	0.00	52.1	42.3	5.7
18	HS = β_0 + SA + Age + YR + ϵ	14	-131.99	293.93	14.71	0.00	65.8	31.4	2.8
13	HS = β_0 + SA + YR + Age + Mast + TPCP _(APR & MAY) + MMNT _(MAR & APR) + (Mast*MMNT _(MAR & APR)) + ϵ	18	-127.42	294.08	14.86	0.00	70.2	27.6	2.3
20	HS = β_0 + SA + YR + Age + TPCP _(APR & MAY) + MMNT _(MAR & APR) + (TPCP _(APR & MAY) * TPCP _(APR & MAY)) + ϵ	17	-129.51	295.90	16.68	0.00	67.6	30.1	2.3
Global	HS = β_0 + SA + YR + (SA*YR) + ϵ	32	-112.01	298.75	19.52	0.00	75.5	19.2	5.3
21	HS = β_0 + SA + YR + Age + DP10 _(APR & MAY) + MMNT _(MAR & APR) + (DP10 _(APR & MAY) * DP10 _(APR & MAY)) + ϵ	17	-131.85	300.59	21.37	0.00	65.4	31.2	3.4

^a Concordance**^b Discordance**

Table 18. *A-priori* models and results of information theoretic model selection process for ruffed grouse chick survival to 35-days post-hatch in the southern and central Appalachian region, 1997-2002, ($n = 145$). Models were fit using linear regression.

Model	Description	K	RSS	Log L	AIC _c	Δ_i	ω_i	R^2	R^2_{adj}
4	$S_{35} = \beta_0 + \text{Mast}$	3	7.559	181.08	-355.99	0.00	0.31	0.04	0.03
2	$S_{35} = \beta_0 + \text{Forest}$	3	7.707	179.83	-353.49	2.50	0.09	0.02	0.01
7	$S_{35} = \beta_0 + \text{DP10}_{(\text{Jun})} + \text{DP10}_{(\text{Jun})}^2$	4	7.603	180.71	-353.13	2.86	0.07	0.03	0.02
5	$S_{35} = \beta_0 + \text{DP10}_{(\text{May})} + \text{DP10}_{(\text{May})}^2$	4	7.605	180.68	-353.08	2.91	0.07	0.03	0.02
Null	$S_{35} = \beta_0$	2	7.862	178.56	-353.04	2.95	0.07	0.00	0.00
9	$S_{35} = \beta_0 + \text{Mast} + \text{Forest} + \text{Mast*Forest}$	5	7.503	181.55	-352.67	3.32	0.06	0.05	0.03
17	$S_{35} = \beta_0 + \text{INCD} + \text{Forest} + \text{INCD*Forest}$	5	7.510	181.49	-352.55	3.44	0.06	0.04	0.02
14	$S_{35} = \beta_0 + \text{DP10}_{(\text{Jun})} + \text{MMNT}_{(\text{Jun})} + \text{DP10}_{(\text{Jun})} * \text{MMNT}_{(\text{Jun})}$	5	7.560	181.06	-351.70	4.29	0.04	0.04	0.02
13	$S_{35} = \beta_0 + \text{DP10}_{(\text{May})} + \text{MMNT}_{(\text{May})} + \text{DP10}_{(\text{May})} * \text{MMNT}_{(\text{May})}$	5	7.576	180.93	-351.43	4.56	0.03	0.04	0.02
3	$S_{35} = \beta_0 + \text{INCD}$	3	7.838	178.76	-351.34	4.64	0.03	0.00	0.00
8	$S_{35} = \beta_0 + \text{MMNT}_{(\text{Jun})}$	3	7.844	178.70	-351.24	4.75	0.03	0.00	0.00
6	$S_{35} = \beta_0 + \text{MMNT}_{(\text{May})}$	3	7.848	178.67	-351.17	4.82	0.03	0.00	0.00
1	$S_{35} = \beta_0 + \text{Age}$	3	7.862	178.56	-350.96	5.03	0.03	0.00	0.00
18	$S_{35} = \beta_0 + \text{Forest} + \text{SA}(\text{Forest})$	10	6.981	186.17	-350.69	5.30	0.02	0.11	0.06
20	$S_{35} = \beta_0 + \text{SA}$	10	6.981	186.17	-350.69	5.30	0.02	0.11	0.06

Table 18. Continued.

Model	Description	K	RSS	Log L	AIC _c	Δ_i	ω_i	R ²	R ² _{adj}
11	$S_{35} = \beta_0 + DP10_{(May)} + MMNT_{(May)} + DP10_{(Jun)} +$ $MMNT_{(Jun)} + (DP10_{(May)} * MMNT_{(May)}) +$ $(DP10_{(Jun)} * MMNT_{(Jun)})$	8	7.341	182.94	-348.83	7.16	0.01	0.07	0.03
19	$S_{35} = \beta_0 + Mast + Forest + SA(Forest)$	11	6.957	186.38	-348.78	7.21	0.01	0.12	0.06
10	$S_{35} = \beta_0 + INCD + DP10_{(May)} + MMNT_{(May)} +$ $DP10_{(Jun)} + MMNT_{(Jun)} +$ $(DP10_{(May)} * MMNT_{(May)}) + (DP10_{(Jun)} * MMNT_{(Jun)})$	9	7.221	184.00	-348.67	7.32	0.01	0.08	0.03
15	$S_{35} = \beta_0 + YR$	6	7.643	180.36	-348.12	7.87	0.01	0.00	0.00
16	$S_{35} = \beta_0 + YR + Forest + YR*Forest$	11	7.108	185.01	-346.04	9.95	0.00	0.04	0.04
22	$S_{35} = \beta_0 + INCD + DP10_{(Jun)} + MMNT_{(Jun)} + Mast$ $+ Forest + SA(Forest) + Mast*Forest$	15	6.595	189.81	-345.90	10.09	0.00	0.16	0.08
21	$S_{35} = \beta_0 + SA + YR$	14	6.776	188.08	-344.92	11.07	0.00	0.11	0.06
Global	$S_{35} = \beta_0 + Age + Forest + SA(Forest) + INCD +$ $DP10_{(May)} + MMNT_{(May)} + DP10_{(Jun)} +$ $MMNT_{(Jun)} + Mast + Mast*Forest$	18	6.288	192.86	-344.28	11.70	0.00	0.20	0.10
12	$S_{35} = \beta_0 + Mast + Forest + Age + Mast*Forest +$ $Mast*Age + Age*Forest + Mast*Forest*Age$	9	7.483	181.72	-344.10	11.88	0.00	0.05	0.00

Table 19. Mean annual survival rates (pooled across sex and age classes) of ruffed grouse in the southern and central Appalachian region by study area and averaged across years. Estimates were obtained using the Kaplan-Meier product limit estimator in Program MARK. Sample size (n) refers to the number of years.

Study Site	n	\bar{x}	S.E.	95% C.I.
KY1	5	0.40	0.03	0.34 – 0.46
MD1	5	0.35	0.017	0.32 – 0.38
NC1	2	0.33	0.045	0.24 – 0.42
OH1	2	0.55	0.025	0.50 – 0.62
OH2	2	0.17	0.085	0.00 – 0.34
PA1	3	0.29	0.044	0.20 – 0.38
RI1	2	0.30	0.09	0.12 – 0.48
VA1	4	0.56	0.037	0.49 – 0.63
VA2	5	0.49	0.063	0.37 – 0.61
VA3	5	0.33	0.05	0.23 – 0.43
WV1	5	0.47	0.047	0.38 – 0.56
WV2	5	0.57	0.071	0.43 – 0.72

Table 20. A-priori models and model selection results of ruffed grouse survival in the southern and central Appalachian region, April 1997 – March 2002. Estimate of over-dispersion (\hat{C}) was 3.14. The analysis was conducted using a seasonal time step corresponding to spring (April – June), summer (July – September), fall (October – December), and winter (January – March). Analysis was completed using the known-fates model with covariates in Program MARK with 1064 individual records.

Model	Description	K	QAIC _c	Δ_i	ω_i
5	$S = \beta_0 + \text{Forest} + \text{Season} (\text{cloglog}) + \epsilon$	22	1937.87	0.00	0.48
14	$S = \beta_0 + \text{Forest} + \text{Age} + \text{Season} (\text{cloglog}) + \epsilon$	23	1938.77	0.90	0.30
15	$S = \beta_0 + \text{Forest} + \text{Sex} + \text{Season} (\text{logit}) + \epsilon$	23	1941.13	3.26	0.09
1	$S = \beta_0 + \text{Season} + \epsilon$	20	1942.58	4.70	0.05
13	$S = \beta_0 + \text{Forest} + \text{Age} + \text{Sex} + \text{Age*Sex} (\text{cloglog}) + \epsilon$	25	1942.60	4.72	0.04
3	$S = \beta_0 + \text{Age} + \text{Season} + \epsilon$	22	1945.29	7.41	0.01
2	$S = \beta_0 + \text{SA} + \text{Season} (\text{cloglog}) + \epsilon$	26	1946.32	8.45	0.01
4	$S = \beta_0 + \text{Sex} + \text{Season} + \epsilon$	22	1946.51	8.63	0.01
16	$S = \beta_0 + \text{Site} + \text{Age} + \text{Season} (\text{logit}) + \epsilon$	27	1946.88	9.01	0.01
17	$S = \beta_0 + \text{Site} + \text{Sex} + \text{Season} (\text{cloglog}) + \epsilon$	27	1947.68	9.81	0.00
7	$S = \beta_0 + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Season} (\text{cloglog}) + \epsilon$	24	1949.18	11.30	0.00
12	$S = \beta_0 + \text{SA} + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Season} (\text{cloglog}) + \epsilon$	29	1950.72	12.84	0.00
8	$S = \beta_0 + \text{Mass} + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Season} + \epsilon$	25	1951.13	13.26	0.00
10	$S = \beta_0 + \text{Forest} + \text{Mast} + \text{Sex} + \text{Age} + \text{Season} + \epsilon$	44	1971.76	33.89	0.00

Table 20. Continued.

Model	Description	K	QAIC _c	Δ_i	ω_i
6	$S = \beta_0 + \text{Mast} + \text{Season} + \varepsilon$	41	1973.41	35.54	0.00
Null	$S = \beta_0 + \varepsilon$	1	2011.31	73.44	0.00
11	$S = \beta_0 + \text{SA} + \varepsilon$	6	2012.78	74.91	0.00
Global	$S = \beta_0 + \text{SA} + \text{Season} + \text{SA} * \text{Season} + \varepsilon$	120	2096.89	159.02	0.00
9	$S = \beta_0 + \text{Forest} + \text{Mast} + \text{Season} + \varepsilon$	42	2536.92	599.04	0.00

Table 21. *A-priori* models and model selection results of ruffed grouse survival (S) in the southern and central Appalachian region, 1997–1998. Estimate of over-dispersion (\hat{c}) was 2.45. Analysis was conducted using a seasonal time step corresponding to spring (April – June), summer (July – September), fall (October – December), and winter (January – March).

Model	Description	K	QAIC _c	Δ_i	ω_i
2	$S = \beta_0 + \text{Season} + \varepsilon$	4	499.11	0.00	0.59
6	$S = \beta_0 + \text{Forest} + \text{Season} + \varepsilon$	6	502.04	2.93	0.14
5	$S = \beta_0 + \text{Sex} + \text{Season} + \varepsilon$	6	502.24	3.13	0.12
4	$S = \beta_0 + \text{Age} + \text{Season} + \varepsilon$	6	502.78	3.67	0.09
8	$S = \beta_0 + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Season} + \varepsilon$	8	505.59	6.48	0.02
7	$S = \beta_0 + \text{Mast} + \text{Season} + \varepsilon$	9	506.12	7.01	0.02
3	$S = \beta_0 + \text{SA} + \text{Season} + \varepsilon$	9	506.92	7.81	0.01
12	$S = \beta_0 + \text{Forest} + \text{Age} + \text{Sex} + \text{Rapt} + \text{Prey} + \text{Rapt*Prey} + \text{Season} + \varepsilon$	12	509.30	10.19	0.00
14	$S = \beta_0 + \text{Forest} + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Snow} + \text{MMNT} + \text{Snow*MMNT} + \text{Season} + \varepsilon$	12	509.30	10.19	0.00
10	$S = \beta_0 + \text{Forest} + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Mast} + \text{Forest* Mast} + \text{Season} + \varepsilon$	13	512.45	13.34	0.00
9	$S = \beta_0 + \text{Forest} + \text{Mast} + \text{Forest* Mast} + \text{Season} + \varepsilon$	14	515.23	16.12	0.00
12	$S = \beta_0 + \text{SA} + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Rapt} + \text{Prey} + \text{Rapt*Prey} + \text{Season} + \varepsilon$	15	515.47	16.36	0.00
13	$S = \beta_0 + \text{SA} + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Snow} + \text{MMNT} + \text{Snow*MMNT} + \text{Season} + \varepsilon$	15	515.54	16.43	0.00

Table 21. Continued.

Model	Description	K	QAIC _c	Δ_i	ω_i
Null	$S = \beta_0 + \varepsilon$	1	520.74	21.63	0.00
Global	$S = \beta_0 + SA + Season + SA*Season + \varepsilon$	20	525.63	26.52	0.00
1	$S = \beta_0 + SA + \varepsilon$	5	526.22	27.11	0.00

Table 22. *A-priori* models and model selection results of ruffed grouse survival (S) in the southern and central Appalachian region, 1998-1999. Estimate of over-dispersion (\hat{c}) was 2.07. Analysis was conducted using a seasonal time step corresponding to spring (April – June), summer (July – September), fall (October – December), and winter (January – March).

Model	Description	K	QAIC _c	Δ_i	ω_i
2	$S = \beta_0 + \text{Season} + \varepsilon$	4	584.94	0.00	0.24
8	$S = \beta_0 + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Season} + \varepsilon$	8	585.03	0.09	0.23
14	$S = \beta_0 + \text{Forest} + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Snow} + \text{MMNT}(\text{win}) + \text{Snow*MMNT}(\text{win}) + \text{Season} + \varepsilon$	12	585.37	0.43	0.20
4	$S = \beta_0 + \text{Age} + \text{Season} + \varepsilon$	6	585.42	0.48	0.19
5	$S = \beta_0 + \text{Sex} + \text{Season} + \varepsilon$	6	588.18	3.24	0.05
12	$S = \beta_0 + \text{SA} + \text{Age} + \text{Sex} + \text{Raptor} + \text{Prey} + \text{Raptor*Prey} + \text{Season} + \varepsilon$	12	588.82	3.87	0.04
6	$S = \beta_0 + \text{Forest} + \text{Season} + \varepsilon$	6	588.92	3.97	0.03
13	$S = \beta_0 + \text{SA} + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Snow} + \text{MMNT}(\text{win}) + \text{Snow*MMNT}(\text{win}) + \text{Season} + \varepsilon$	16	592.26	7.32	0.01
3	$S = \beta_0 + \text{SA} + \text{Season} + \varepsilon$	10	593.50	8.55	0.00
7	$S = \beta_0 + \text{Mast} + \text{Season} + \varepsilon$	9	593.82	8.88	0.00
10	$S = \beta_0 + \text{Forest} + \text{Mast} + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Season} + \varepsilon$	13	593.91	8.97	0.00
11	$S = \beta_0 + \text{SA} + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Raptor} + \text{Prey} + \text{Raptor*Prey} + \text{Season} + \varepsilon$	16	595.51	10.56	0.00

Table 22. Continued.

Model	Description	K	QAIC _c	Δ_i	ω_i
9	$S = \beta_0 + \text{Forest} + \text{Mast} + \text{Forest}*\text{Mast} + \text{Season} + \varepsilon$	14	601.15	16.21	0.00
Null	$S = \beta_0 + \varepsilon$	1	604.05	19.11	0.00
1	$S = \beta_0 + \text{SA} + \varepsilon$	6	610.57	25.62	0.00
Global	$S = \beta_0 + \text{SA} + \text{Season} + \text{SA}*\text{Season} + \varepsilon$	24	619.84	34.90	0.00

Table 23. *A-priori* models and model selection results of ruffed grouse survival (S) in the southern and central Appalachian region, 1999-2000. The estimate of over-dispersion (\hat{c}) was 2.06. Analysis was conducted using a seasonal time step corresponding to spring (April – June), summer (July – September), fall (October – December), and winter (January – March).

Model	Description	K	QAIC _c	Δ_i	ω_i
12	$S = \beta_0 + \text{Forest} + \text{Age} + \text{Sex} + \text{Raptor} + \text{Prey} + \text{Raptor*Prey} + \text{Season} + \varepsilon$	12	727.89	0.00	0.40
14	$S = \beta_0 + \text{Forest} + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Snow} + \text{MMNT}(\text{win}) + \text{Snow*MMTN}(\text{Win}) + \text{Season} + \varepsilon$	12	729.26	1.37	0.20
6	$S = \beta_0 + \text{Forest} + \text{Season} + \varepsilon$	6	729.41	1.53	0.19
9	$S = \beta_0 + \text{Forest} + \text{Mast} + \text{Forest*Mast} + \text{Season} + \varepsilon$	14	729.78	1.90	0.16
10	$S = \beta_0 + \text{Forest} + \text{Mast} + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Season} + \varepsilon$	13	733.10	5.22	0.03
4	$S = \beta_0 + \text{Age} + \text{Season} + \varepsilon$	6	734.99	7.11	0.01
7	$S = \beta_0 + \text{Mast} + \text{Season} + \varepsilon$	9	738.05	10.17	0.00
8	$S = \beta_0 + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Season} + \varepsilon$	8	738.61	10.73	0.00
5	$S = \beta_0 + \text{Sex} + \text{Season} + \varepsilon$	6	738.89	11.00	0.00
3	$S = \beta_0 + \text{SA} + \text{Season} + \varepsilon$	11	739.39	11.51	0.00
11	$S = \beta_0 + \text{SA} + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Raptor} + \text{Prey} + \text{Raptor*Prey} + \text{Season} + \varepsilon$	17	743.16	15.27	0.00

Table 23. Continued.

Model	Description	K	QAIC _c	Δ_i	ω_i
13	$S = \beta_0 + SA + Age + Sex + Age*Sex + Snow + MMNT(win) + Snow*MMNT(win) + Season + \varepsilon$	17	745.39	17.51	0.00
2	$S = \beta_0 + Season + \varepsilon$	4	1506.23	778.34	0.00
Global	$S = \beta_0 + SA + Season + SA*Season + \varepsilon$	28	1516.25	788.36	0.00
1	$S = \beta_0 + SA + \varepsilon$	7	1527.11	799.22	0.00
Null	$S = \beta_0 + \varepsilon$	1	1536.42	808.54	0.00

Table 24. Estimates of seasonal survival rates in oak-hickory and mixed-mesophytic forests, 1999 – 2000 in the southern and central Appalachian region based on 3 competing *a-priori* models.

Model	Season	Forest			
		Oak-Hickory		Mixed-Mesophytic	
		\bar{x}	95% CI	\bar{x}	95% CI
12	Spring	0.83	0.77-0.88	0.76	0.66-0.84
	Summer	0.93	0.89-0.95	0.90	0.83-0.94
	Fall	0.82	0.77-0.86	0.75	0.65-0.83
	Winter	0.83	0.69-0.91	0.76	0.56-0.89
14	Spring	0.84	0.83-0.85	0.80	0.78-0.81
	Summer	0.93	0.91-0.95	0.91	0.89-0.93
	Fall	0.82	0.79-0.84	0.77	0.74-0.80
	Winter	0.84	0.79-0.88	0.79	0.73-0.84
6	Spring	0.87	0.82-0.91	0.82	0.73-0.88
	Summer	0.94	0.91-0.96	0.91	0.85-0.95
	Fall	0.80	0.74-0.85	0.74	0.63-0.82
	Winter	0.85	0.43-0.98	0.80	0.31-0.97

Table 25. *A-priori* models and model selection results of ruffed grouse survival (S) in the southern and central Appalachian region, 2000-2001. Estimate of over-dispersion (\hat{c}) was 1.94. Analysis was conducted using a seasonal time step corresponding to spring (April – June), summer (July – September), fall (October – December), and winter (January – March).

Model	Description	K	QAIC _c	Δ_i	ω_i
9	$S = \beta_0 + \text{Forest} + \text{Mast} + \text{Forest} * \text{Mast} + \text{Season} + \varepsilon$	14	592.49	0.00	0.65
6	$S = \beta_0 + \text{Forest} + \text{Season} + \varepsilon$	6	595.37	2.88	0.15
10	$S = \beta_0 + \text{Forest} + \text{Mast} + \text{Age} + \text{Sex} + \text{Age} * \text{Sex} + \text{Season} + \varepsilon$	13	596.43	3.94	0.09
12	$S = \beta_0 + \text{Forest} + \text{Age} + \text{Sex} + \text{Raptor} + \text{Prey} + \text{Raptor} * \text{Prey} + \text{Season} + \varepsilon$	12	598.52	6.03	0.03
14	$S = \beta_0 + \text{Forest} + \text{Age} + \text{Sex} + \text{Age} * \text{Sex} + \text{Snow} + \text{MMNT}(\text{win}) + \text{Snow} * \text{MMTN}(\text{Win}) + \text{Season} + \varepsilon$	12	598.52	6.03	0.03
4	$S = \beta_0 + \text{Age} + \text{Season} + \varepsilon$	6	600.01	7.52	0.02
2	$S = \beta_0 + \text{Season} + \varepsilon$	4	600.21	7.72	0.01
5	$S = \beta_0 + \text{Sex} + \text{Season} + \varepsilon$	6	602.06	9.57	0.01
8	$S = \beta_0 + \text{Age} + \text{Sex} + \text{Age} * \text{Sex} + \text{Season} + \varepsilon$	8	602.35	9.86	0.00
3	$S = \beta_0 + \text{SA} + \text{Season} + \varepsilon$	9	603.13	10.65	0.00
11	$S = \beta_0 + \text{SA} + \text{Age} + \text{Sex} + \text{Age} * \text{Sex} + \text{Raptor} + \text{Prey} + \text{Raptor} * \text{Prey} + \text{Season} + \varepsilon$	15	604.77	12.28	0.00
7	$S = \beta_0 + \text{SA} + \text{Age} + \text{Sex} + \text{Age} * \text{Sex} + \text{Raptor} + \text{Prey} + \text{Raptor} * \text{Prey} + \text{Season} + \varepsilon$	9	608.10	15.62	0.00

Table 25. Continued.

Model	Description	K	QAIC _c	Δ_i	ω_i
13	$S = \beta_0 + SA + Age + Sex + Age*Sex + Snow + MMNT(win) + Snow*MMNT(win) + Season + \varepsilon$	15	608.41	15.92	0.00
Null	$S = \beta_0$	1	613.59	21.10	0.00
Global	$S = \beta_0 + SA + Season + SA*Season + \varepsilon$	20	613.68	21.19	0.00
1	$S = \beta_0 + SA + \varepsilon$	5	615.43	22.94	0.00

Table 26. Ruffed grouse seasonal and annual survival rates on oak-hickory (OH) and mixed-mesophytic (MM) forests in the southern and central Appalachian region using Model 9, April 2000 – March 2001.

Season	Forest Association			
	OH		MM	
	Mean	95% C.I.	Mean	95% C.I.
Spring	0.66	0.54 – 0.77	0.56	0.42 – 0.71
Summer	0.96	0.91 – 0.99	0.92	0.82 – 0.98
Fall	0.88	0.77 – 0.95	0.80	0.65 – 0.92
Winter	0.87	0.76 – 0.94	0.79	0.64 – 0.91
Annual	0.49	0.29 – 0.68	0.33	0.14 – 0.58

Table 27. *A-priori* models and model selection results of ruffed grouse survival (S) in the southern and central Appalachian region, 2001-2002. Estimate of over-dispersion (\hat{c}) was 2.09. Analysis was conducted using a seasonal Season step corresponding to spring (April – June), summer (July – September), fall (October – December), and winter (January – March).

Model	Description	K	QAIC _c	Δ_i	ω_i
2	$S = \beta_0 + \text{Season} + \varepsilon$	4	278.80	0.00	0.39
6	$S = \beta_0 + \text{Forest} + \text{Season} + \varepsilon$	6	279.16	0.36	0.32
8	$S = \beta_0 + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Season} + \varepsilon$	8	281.72	2.92	0.09
4	$S = \beta_0 + \text{Age} + \text{Season} + \varepsilon$	6	282.76	3.96	0.05
5	$S = \beta_0 + \text{Sex} + \text{Season} + \varepsilon$	6	282.83	4.04	0.05
10	$S = \beta_0 + \text{Forest} + \text{Mast} + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Season} + \varepsilon$	13	284.06	5.26	0.03
3	$S = \beta_0 + \text{SA} + \text{Season} + \varepsilon$	8	284.08	5.28	0.03
14	$S = \beta_0 + \text{SA} + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{SNOW} + \text{MMNT}(\text{Win}) + \text{SNOW*MMNT}(\text{Win}) + \text{Season} + \varepsilon$	12	285.49	6.69	0.01
12	$S = \beta_0 + \text{Forest} + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{SNOW} + \text{MMNT}(\text{Win}) + \text{SNOW*MMNT}(\text{Win}) + \text{Season} + \varepsilon$	12	285.49	6.69	0.01
9	$S = \beta_0 + \text{Forest} + \text{Mast} + \text{Forest*Mast} + \text{Season} + \varepsilon$	14	288.13	9.33	0.00
7	$S = \beta_0 + \text{Mast} + \text{Season} + \varepsilon$	9	288.51	9.71	0.00

Table 27. Continued.

Model	Description	K	QAIC _c	Δ_i	ω_i
1	$S = \beta_0 + SA + \varepsilon$	3	289.22	10.42	0.00
13	$S = \beta_0 + SA + Age + Sex + Age*Sex + SNOW + MMNT_{(Win)} + SNOW*MMNT_{(Win)} + Season + \varepsilon$	14	289.65	10.85	0.00
11	$S = \beta_0 + SA + Age + Sex + Age*Sex + Raptor + Prey + Raptor*Prey + Season + \varepsilon$	14	289.65	10.85	0.00
Null	$S = \beta_0 + \varepsilon$	1	290.12	11.32	0.00
Global	$S = \beta_0 + SA + Season + SA*Season + \varepsilon$	16	298.87	20.07	0.00

Table 28. *A-priori* models and results of model selection process of ruffed grouse survival during fall (Oct.-Dec.) in the southern and central Appalachian region, 1996 - 2001. Estimate of over-dispersion (\hat{c}) was 1.35. Analysis was conducted using a monthly time step.

Model	Description	K	QAIC _c	Δ_i	ω_i
14	$S = \beta_0 + SA + Age + Sex + Age*Sex + Year + Month + \varepsilon$ (cloglog)	19	1789.18	0.00	0.60
5	$S = \beta_0 + Age + Year + Month + \varepsilon$	9	1791.57	2.38	0.18
9	$S = \beta_0 + Age + Sex + Age*Sex + Year + Month + \varepsilon$	11	1791.59	2.41	0.18
7	$S = \beta_0 + Forest + Year + Month + \varepsilon$	9	1795.98	6.79	0.02
10	$S = \beta_0 + Forest + Mast + Forest*Mast + Month + \varepsilon$	7	1798.38	9.20	0.01
11	$S = \beta_0 + Forest + Age + Sex + Age*Sex + Mast + Month + \varepsilon$	9	1799.22	10.03	0.00
4	$S = \beta_0 + SA + Year + Month + \varepsilon$	16	1799.72	10.54	0.00
13	$S = \beta_0 + Forest + Age + Sex + Age*Sex + Raptor + Prey + Raptor*Prey + Month + \varepsilon$	11	1800.34	11.15	0.00
12	$S = \beta_0 + SA + Age + Sex + Age*Sex + Raptor + Prey + Raptor*Prey + Month + \varepsilon$	18	1801.82	12.64	0.00
6	$S = \beta_0 + Sex + Year + Month + \varepsilon$	9	1803.63	14.45	0.00
3	$S = \beta_0 + SA + Month + \varepsilon$	12	1806.92	17.73	0.00
1	$S = \beta_0 + SA + \varepsilon$	9	1807.24	18.05	0.00
2	$S = \beta_0 + Month + \varepsilon$	3	1808.67	19.49	0.00
Null	$S = \beta_0 + \varepsilon$	1	1810.49	21.30	0.00
8	$S = \beta_0 + Mast + Month + \varepsilon$	5	1812.57	23.39	0.00
Global	$S = \beta_0 + SA + Month + SA*Month + \varepsilon$	27	1814.32	25.13	0.00

Table 29. *A-priori* models and results of model selection process of ruffed grouse survival during winter (Jan. – Mar.) in the southern and central Appalachian region, 1997 - 2002. Estimate of over-dispersion (\hat{c}) was 1.37. Analysis was conducted using a monthly time step.

Model	Description	K	QAIC _c	Δ_i	ω_i
5	$S = \beta_0 + \text{Age} + \text{year} + \text{Month} + \varepsilon$ (cloglog)	9	1517.44	0.00	0.41
9	$S = \beta_0 + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Year} + \text{Month} + \varepsilon$ (cloglog)	11	1518.35	0.91	0.26
7	$S = \beta_0 + \text{Forest} + \text{Year} + \text{Month} + \varepsilon$ (cloglog)	9	1519.21	1.77	0.17
6	$S = \beta_0 + \text{Sex} + \text{Year} + \text{Month} + \varepsilon$	9	1519.26	1.82	0.16
4	$S = \beta_0 + \text{SA} + \text{Year} + \text{Month} + \varepsilon$	16	1530.91	13.47	0.00
17	$S = \beta_0 + \text{Forest} + \text{Mast} + \text{MMNT} + \text{Snow} + \text{MMNT*Snow} + \text{Month} + \varepsilon$	9	1534.80	17.35	0.00
12	$S = \beta_0 + \text{Forest} + \text{Mast} + \text{MMNT} + \text{Mast*MMNT} + \text{Month} + \varepsilon$	8	1541.25	23.81	0.00
13	$S = \beta_0 + \text{Forest} + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Mast} + \text{MMNT} + \text{Mast*MMNT} + \text{Month} + \varepsilon$	11	1541.77	24.33	0.00
10	$S = \beta_0 + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{MMNT} + \text{Month} + \varepsilon$ (cloglog)	8	1542.30	24.86	0.00
19	$S = \beta_0 + \text{Mast} + \text{MMNT} + \text{Mast*MMNT} + \text{Month} + \varepsilon$	7	1543.49	26.04	0.00
20	$S = \beta_0 + \text{Age} + \text{Sex} + \text{Age*Sex} + \text{Mast} + \text{MMNT} + \text{Mast*MMNT} + \text{Month} + \varepsilon$ (cloglog)	10	1544.90	27.46	0.00
16	$S = \beta_0 + \text{SA} + \text{MMNT} + \text{Snow} + \text{MMNT*Snow} + \text{Month} + \varepsilon$	15	1545.28	27.84	0.00
21	$S = \beta_0 + \text{SA} + \text{Mast} + \text{MMNT} + \text{Snow} + \text{Snow*MMNT} + \text{Month} + \varepsilon$	16	1547.24	29.80	0.00

Table 29. Continued.

Model	Description	K	QAIC_c	Δ_i	ω_i
Null	$S = \beta_0 + \varepsilon$	1	1548.86	31.42	0.00
8	$S = \beta_0 + \text{Mast} + \text{Month} + \varepsilon$	5	1549.22	31.77	0.00
2	$S = \beta_0 + \text{Month} + \varepsilon$	3	1549.32	31.88	0.00
11	$S = \beta_0 + \text{Forest} + \text{Mast} + \text{Mast*Forest} + \text{Month} + \varepsilon$	7	1551.28	33.83	0.00
14	$S = \beta_0 + \text{Forest} + \text{Raptor} + \text{Prey} + \text{Raptor*Prey} + \text{Month} + \varepsilon$	8	1555.42	37.98	0.00
22	$S = \beta_0 + \text{SA} + \text{Mast} + \text{MMNT} + \text{Mast*MMNT} + \text{Month} + \varepsilon$	15	1556.48	39.03	0.00
1	$S = \beta_0 + \text{SA} + \varepsilon$	9	1563.90	46.46	0.00
3	$S = \beta_0 + \text{SA} + \text{Month} + \varepsilon$	12	1566.36	48.92	0.00
15	$S = \beta_0 + \text{SA} + \text{Raptor} + \text{Prey} + \text{Raptor*Prey} + \text{Month} + \varepsilon$	15	1568.01	50.57	0.00
18	$S = \beta_0 + \text{SA} + \text{Mast} + \text{SA*Mast} + \text{Month} + \varepsilon$	16	1569.89	52.45	0.00
Global	$S = \beta_0 + \text{SA} + \text{Month} + \text{SA*Month} + \varepsilon$	27	1583.80	66.36	0.00

Table 30. *A-priori* models and results of model selection process of ruffed grouse survival during spring (Apr. - June) in the southern and central Appalachian region, 1997 - 2002. Estimate of over-dispersion (\hat{c}) was 1.35. Analysis was conducted using a monthly time step.

Model	Description	K	QAIC _c	Δ_i	ω_i
6	$S = \beta_0 + \text{Sex} + \text{Year} + \text{Month} + \varepsilon$	9	1587.30	0.00	0.42
18	$S = \beta_0 + \text{Age} + \text{Sex} + \text{Year} + \text{Month} + \varepsilon$ (cloglog)	10	1587.60	0.30	0.36
10	$S = \beta_0 + \text{Age} + \text{Sex} + \text{Age}*\text{sex} + \text{Year} + \text{Month} + \varepsilon$ (cloglog)	11	1589.04	1.75	0.18
12	$S = \beta_0 + \text{Forest} + \text{Age} + \text{Sex} + \text{Age}*\text{Sex} + \text{Mast} + \text{Month} + \varepsilon$	9	1592.18	4.89	0.04
15	$S = \beta_0 + \text{SA} + \text{Age} + \text{Sex} + \text{Age}*\text{Sex} + \text{Mast} + \text{Month} + \varepsilon$	16	1598.16	10.86	0.00
5	$S = \beta_0 + \text{Age} + \text{Year} + \text{Month} + \varepsilon$	9	1600.59	13.30	0.00
3	$S = \beta_0 + \text{Year} + \text{Month} + \varepsilon$	8	1603.03	15.74	0.00
7	$S = \beta_0 + \text{Forest} + \text{Year} + \text{Month} + \varepsilon$	9	1605.04	17.74	0.00
8	$S = \beta_0 + \text{Mast} + \text{Month} + \varepsilon$	5	1608.60	21.30	0.00
11	$S = \beta_0 + \text{Forest} + \text{Mast} + \text{Forest}*\text{Mast} + \text{Month} + \varepsilon$	7	1608.75	21.45	0.00
4	$S = \beta_0 + \text{SA} + \text{Year} + \text{Month} + \varepsilon$	16	1611.14	23.84	0.00
2	$S = \beta_0 + \text{Month} + \varepsilon$	3	1612.99	25.69	0.00
9	$S = \beta_0 + \text{TPCP} + \text{Month} + \varepsilon$	5	1615.45	28.15	0.00
13	$S = \beta_0 + \text{Forest} + \text{TPCP} + \text{Month} + \varepsilon$	5	1615.57	28.28	0.00
17	$S = \beta_0 + \text{Forest} + \text{Raptor} + \text{Prey} + \text{Raptor}*\text{Prey} + \text{Month} + \varepsilon$	8	1620.43	33.13	0.00

Table 30. Continued.

Model	Description	K	QAIC _c	Δ_i	ω_i
16	$S = \beta_0 + SA + TPCP + Month + \varepsilon$	13	1624.66	37.36	0.00
14	$S = \beta_0 + SA + Raptor + Prey + Raptor*Prey + \varepsilon$	15	1627.07	39.78	0.00
Global	$S = \beta_0 + SA + Month + SA*Month + \varepsilon$	27	1645.35	58.06	0.00
Null	$S = \beta_0 + \varepsilon$	1	1662.71	75.42	0.00
1	$S = \beta_0 + SA + \varepsilon$	9	1670.67	83.38	0.00

Table 31. Estimates of male and female monthly survival rates in spring in the southern and central Appalachian region, 1997 – 2000 based on model 6 (Table 30).

Year	Season	Sex			
		Female		Male	
		\bar{x}	95% CI	\bar{x}	95% CI
1997	April	0.89	0.88-0.90	0.92	0.91-0.93
	May	0.91	0.89-0.92	0.93	0.92-0.94
	June	0.97	0.96-0.98	0.98	0.97-0.98
1998	April	0.91	0.90-0.92	0.93	0.92-0.94
	May	0.93	0.91-0.94	0.94	0.93-0.96
	June	0.98	0.97-0.98	0.98	0.98-0.99
1999	April	0.89	0.88-0.90	0.92	0.91-0.93
	May	0.91	0.89-0.93	0.93	0.91-0.95
	June	0.97	0.96-0.98	0.98	0.97-0.98
2000	April	0.92	0.91-0.94	0.94	0.93-0.95
	May	0.94	0.92-0.95	0.95	0.94-0.96
	June	0.98	0.97-0.98	0.99	0.98-1.0

Table 32. Estimates of male and female monthly spring survival rates in the southern and central Appalachian region, 1997 – 2000 based on model 18 (Table 30).

Year	Month	Sex			
		Female		Male	
		\bar{x}	95% CI	\bar{x}	95% CI
1997	April	0.89	0.85-0.92	0.91	0.86-0.95
	May	0.91	0.86-0.94	0.93	0.87-0.97
	June	0.97	0.48-1.0	0.98	0.49-1.0
1998	April	0.91	0.87-0.94	0.93	0.89-0.96
	May	0.93	0.88-0.96	0.95	0.90-0.96
	June	0.98	0.51-1.0	0.99	0.53-1.0
1999	April	0.89	0.85-0.93	0.92	0.86-0.95
	May	0.91	0.86-0.95	0.93	0.87-0.97
	June	0.97	0.48-1.0	0.98	0.49-1.0
2000	April	0.92	0.88-0.95	0.94	0.89-0.97
	May	0.93	0.89-0.96	0.95	0.90-0.98
	June	0.98	0.52-1.0	0.99	0.54-1.0

Table 33. Estimates of male and female monthly spring survival rates in the southern and central Appalachian region, 1997 – 2000 based on model 10 (Table 30).

Year	Month	Sex			
		Female		Male	
		\bar{x}	95% CI	\bar{x}	95% CI
1997	April	0.89	0.85-0.93	0.91	0.86-0.95
	May	0.91	0.86-0.94	0.93	0.87-0.97
	June	0.97	0.28-1.0	0.98	0.31-1.0
1998	April	0.91	0.87-0.94	0.93	0.87-0.97
	May	0.93	0.89-0.96	0.95	0.90-0.98
	June	0.98	0.32-1.0	0.99	0.33-1.0
1999	April	0.89	0.88-0.93	0.92	0.86-0.96
	May	0.91	0.89-0.95	0.93	0.87-0.97
	June	0.97	0.33-1.0	0.98	0.31-1.0
2000	April	0.92	0.88-0.95	0.94	0.89-0.97
	May	0.93	0.89-0.96	0.95	0.90-0.98
	June	0.98	0.33-1.0	0.99	0.34-1.0

Table 34. *A-priori* models and results of model selection process of ruffed grouse survival during summer (July – Sept.) in the southern and central Appalachian region, 1997 - 2002. Estimate of over-dispersion (\hat{c}) was 0.60. Analysis was conducted using a monthly time step.

Model	Description	K	QAIC _c	Δ_i	ω_i
7	$S = \beta_0 + \text{Forest} + \text{Year} + \text{Month} + \varepsilon$	10	1355.78	0.00	0.55
8	$S = \beta_0 + \text{Forest} + \text{Sex} + \text{Year} + \text{Month} + \varepsilon$	11	1357.73	1.95	0.21
13	$S = \beta_0 + \text{Forest} + \text{Raptor} + \text{Prey} + \text{Raptor*Prey} + \text{Month} + \varepsilon$	8	1358.51	2.73	0.14
10	$S = \beta_0 + \text{Forest} + \text{Sex} + \text{Forest*Sex} + \text{Month} + \varepsilon$	12	1359.65	3.87	0.08
5	$S = \beta_0 + \text{Sex} + \text{Year} + \text{Month} + \varepsilon$	9	1364.96	9.18	0.01
4	$S = \beta_0 + \text{Year} + \text{Month} + \varepsilon$	9	1365.26	9.48	0.00
2	$S = \beta_0 + \text{Month} + \varepsilon$	3	1365.70	9.92	0.00
6	$S = \beta_0 + \text{SA} + \text{Year} + \text{Month} + \varepsilon$	16	1369.88	14.10	0.00
12	$S = \beta_0 + \text{Forest} + \text{Raptor} + \text{Prey} + \text{Raptor*Prey} + \text{Month} + \varepsilon$	14	1370.67	14.89	0.00
9	$S = \beta_0 + \text{SA} + \text{Sex} + \text{Year} + \text{Month} + \varepsilon$	17	1371.80	16.03	0.00
3	$S = \beta_0 + \text{Year} + \varepsilon$	6	1375.78	20.00	0.00
Null	$S = \beta_0 + \varepsilon$	1	1378.21	22.43	0.00
Global	$S = \beta_0 + \text{SA} + \text{Month} + \text{SA*Month} + \varepsilon$	27	1381.43	25.65	0.00
1	$S = \beta_0 + \text{SA} + \varepsilon$	9	1382.65	26.87	0.00

Table 35. Estimates of ruffed grouse monthly summer survival by forest association [oak-hickory (OH) and mixed-mesophytic (MM)] in the southern and central Appalachian region, 1997 – 2001 based on model 7 (Table 34).

Year	Month	Forest			
		OH		MM	
		\bar{x}	95% CI	\bar{x}	95% CI
1997	July	0.96	0.95-0.97	0.95	0.93-0.97
	August	0.98	0.97-0.99	0.98	0.97-0.99
	September	0.96	0.92-0.98	0.95	0.89-0.98
1998	July	0.96	0.94-0.97	0.95	0.92-0.96
	August	0.98	0.97-0.99	0.98	0.96-0.99
	September	0.96	0.91-0.98	0.94	0.87-0.97
1999	July	0.96	0.94-0.97	0.94	0.91-0.96
	August	0.98	0.97-0.99	0.97	0.95-0.98
	September	0.95	0.90-0.98	0.94	0.86-0.97
2000	July	0.96	0.94-0.97	0.94	0.92-0.96
	August	0.98	0.97-0.99	0.97	0.96-0.99
	September	0.96	0.90-0.98	0.94	0.87-0.97
2001	July	0.96	0.94-0.97	0.94	0.92-0.96
	August	0.98	0.97-0.99	0.97	0.96-0.98
	September	0.96	0.91-0.98	0.94	0.87-0.87

Table 36. Estimates of ruffed grouse monthly summer survival by forest association [oak-hickory (OH) and mixed-mesophytic (MM)] in the southern and central Appalachian region, 1997 – 2001 based on model 8 (Table 34).

Year	Month	Forest			
		OH		MM	
		\bar{x}	95% CI	\bar{x}	95% CI
1997	July	0.96	0.95-0.97	0.95	0.94-0.96
	August	0.98	0.98-0.99	0.98	0.97-0.98
	September	0.96	0.95-0.97	0.95	0.94-0.96
1998	July	0.96	0.95-0.97	0.95	0.93-0.96
	August	0.98	0.98-0.99	0.98	0.97-0.98
	September	0.96	0.95-0.96	0.94	0.93-0.95
1999	July	0.96	0.95-0.96	0.94	0.93-0.95
	August	0.98	0.97-0.98	0.97	0.96-0.98
	September	0.95	0.93-0.95	0.94	0.93-0.95
2000	July	0.96	0.95-0.96	0.94	0.93-0.95
	August	0.98	0.98-0.98	0.97	0.97-0.98
	September	0.96	0.95-0.96	0.94	0.93-0.95
2001	July	0.96	0.95-0.97	0.94	0.93-0.95
	August	0.98	0.98-0.98	0.97	0.97-0.98
	September	0.96	0.95-0.96	0.94	0.93-0.95

Table 37. Distribution of hunter harvested (including legal harvest, crippling loss, and illegal harvest) radio-collared birds (pooled across years) on study areas participating in the Appalachian Cooperative Grouse Research Project test of the compensatory mortality hypothesis, 1996 – 2001.

Month	# Harvested	% of Harvest
October	26	22
November	30	26
December	14	12
January	23	20
February	23	20
March	1	<1.0

Table 38. Results of a repeated measures analysis of variance test of the effects of hunting on ruffed grouse annual survival (April – March) pooled across age and sex classes in the southern and central Appalachian region, 1996 – 2002. Analysis was conducted using Proc Mixed (SAS Institute 2000). Phase I was defined as spring 1997 – summer of 1999 during which control and treatment sites were open to hunting. Phase II was defined as fall 1999 – summer 2002 during which treatment sites were closed to hunting.

Source	Numerator df	Denominator df	F	<i>P</i>
Treatment	1	4.0	1.15	0.345
Phase	1	18.3	1.89	0.186
Treatment*Phase	1	18.0	2.48	0.133
Treatment*Year(Phase)	3	18.4	0.22	0.884

Table 39. Stable age distributions used in the development of deterministic and stochastic ruffed grouse population models. Model 1 incorporated multiple variables including nest rate, nest success, re-nest rate, clutch size, hatchability, and chick survival to 35-days post hatch to estimate productivity. Models 2 and the stochastic model estimated productivity with 1 parameter, the mean number of chicks produced at 35-days post hatch per hen alive on 1 April. Table reports proportion of the population in each age class.

Spatial Scale	Models 1				Models 2 & Stochastic Model			
	Age 1	Age 2	Age 3	Age 4	Age 1	Age 2	Age 3	Age 4
Regional ^a	0.492	0.273	0.151	0.084	0.570	0.259	0.118	0.054
Mixed-Mesophytic Forests ^b (MMF)	0.511	0.271	0.143	0.076	0.555	0.262	0.124	0.059
Oak-Hickory Forests ^b (OHF)	0.432	0.277	0.177	0.113	0.554	0.263	0.124	0.059
Mixed-Mesophytic Study Area ^c (MMS)	0.532	0.267	0.134	0.067	0.575	0.258	0.115	0.052
Oak-Hickory Study Area ^c (OHS)	0.447	0.276	0.171	0.106	0.555	0.262	0.124	0.059

^a Parameter estimates at the regional scale were calculated pooling across all study areas and averaging across years.

^b Parameter estimates for mixed-mesophytic and oak-hickory forests were calculated by pooling across study areas identified as dominated by each respective forest association and averaged across years.

^c Parameter estimates for mixed-mesophytic and oak-hickory forest study areas were calculated by averaging across years and study areas identified as dominated by respective forest type.

Table 40. Estimates of ruffed grouse finite population growth rate (λ) and fecundity (F and F') based on 2 alternative deterministic models at 3 spatial scales. Model 1 estimated fecundity (F) as a function of multiple reproductive parameters including nest rate, nest success, clutch size, hatchability, reneest rate, and chick survival to 35-days post-hatch. Model 2 estimated fecundity (F') using 1 parameter (# of chicks alive at 35-days post-hatch/ female alive on 1 April). Models were developed using population vital rates estimated from data collected as part of the Appalachian Cooperative Grouse Research Project, 1996 – 2002.

Scale	Model 1		Model 2	
	λ	F	λ	F'
Regional ^a	0.78	0.66	0.95	0.92
Mixed-mesophytic Forests ^b	0.73	0.69	0.82	0.84
Oak-Hickory Forests ^b	0.79	0.53	1.06	0.91
Mixed-mesophytic Study Area ^c	0.72	0.73	0.81	0.89
Oak-hickory Study Area ^c	0.74	0.54	1.04	0.87

^a Parameter estimates at the regional scale were calculated pooling across all study areas and averaging across years.

^b Parameter estimates for mixed-mesophytic and oak-hickory forests were calculated by pooling across study areas identified as dominated by each respective forest association and averaged across years.

^c Parameter estimates for mixed-mesophytic and oak-hickory forest study areas were calculated by averaging across years and study areas identified as dominated by respective forest type.

Table 41. Estimates of ruffed grouse finite population growth rate (λ) based on 1000 simulations of a stochastic population model. Fecundity (F') was estimated with 1 parameter, the mean number of chicks produced at 35-days post hatch per hen alive on 1 April. The model was developed using population vital rates estimated from data collected as part of the Appalachian Cooperative Grouse Research Project, 1996 – 2002.

Scale	Stochastic Model		
	λ	S.D.	95% CI
Regional ^a	0.922	0.006	0.919 – 0.925
Mixed-mesophytic Forests ^b	0.885	0.006	0.882 – 0.888
Oak-Hickory Forests ^b	1.082	0.002	1.081 – 1.083
Mixed-mesophytic Study Area ^c	0.922	0.008	0.918 – 0.926
Oak-hickory Study Area ^c	1.093	0.003	1.092 – 1.095

^a Parameter estimates at the regional scale were calculated pooling across all study areas and averaging across years.

^b Parameter estimates for mixed-mesophytic and oak-hickory forests were calculated by pooling across study areas identified as dominated by each respective forest association and averaged across years.

^c Parameter estimates for mixed-mesophytic and oak-hickory forest study areas were calculated by averaging across years and study areas identified as dominated by respective forest type.

Table 42. Proportion of model runs that ended with an extant ruffed grouse population after 100 years based on a stochastic population model developed from data collected as part of the ACGRP, 1996 -2002.

Scale	Initial Population Size											
	1,000			5,000			10,000			25,000		
	Proportion Extant	S.E.		Proportion Extant	S.E.		Proportion Extant	S.E.		Proportion Extant	S.E.	
Regional	0.001	0.001		0.013	0.004		0.024	0.005		0.076	0.008	
MMF ^a	0.0	0.000		0.0	0.000		0.0	0.000		0.0	0.000	
OHF ^b	1.0	0.000		1.0	0.000		1.0	0.000		1.0	0.000	
MMS ^c	0.0	0.000		0.0	0.000		0.0	0.000		0.03	0.005	
OHS ^d	1.0	0.000		1.0	0.000		1.0	0.000		1.0	0.000	

^a Mixed-mesophytic forest association scale

^b Oak-hickory forest association scale

^c Mixed-mesophytic forest study area scale

^c Oak-hickory forest study area scale

Table 44. Comparison of ruffed grouse mean population vital rates in oak-hickory and mixed-mesophytic forests in the southern and central Appalachian region, 1996 – 2002 and published estimates from the northern hardwood forests common in the core of ruffed grouse range (e.g., the Great Lakes and southern Canada regions).

Vital Rate	Forest Association		
	Oak-hickory	Mixed-mesophytic	Northern hardwood ^a
	\bar{x}	\bar{x}	\bar{x}
Nesting Rate	86%	100%	100% ^a
Re-nesting Rate	3.2%	45%	≥46% ^b
Clutch Size	9.4 eggs	10.37 eggs	≥11 eggs ^c
Nest Success	63%	70%	≥43% ^d
Chick Survival	21%	39%	≈50% ^e
Adult Annual Survival	≈50%	≈42%	≤37% ^f

^a Holzwardt (1990), Balzer (1995), Small et al. (1996)

^b Rusch and Keith (1971), Larson (1988), Belzar (1995), Small et al. (1996)

^c Fallis and Hope (1950), Cringan (1970), Rusch and Keith (1971), Maxon (1978)

^d Maxon (1978), Rusch and Keith (1971), Holzwardt (1990), Balzer (1995), Small et al. (1996)

^e Marshall and Gullion (1965), Rusch and Keith (1971), Beckerton and Middleton (1982)

^f Rusch and Keith 1971, Dorney and Kabat 1960, Small et al. 1991, Gutierrez et al. 2003

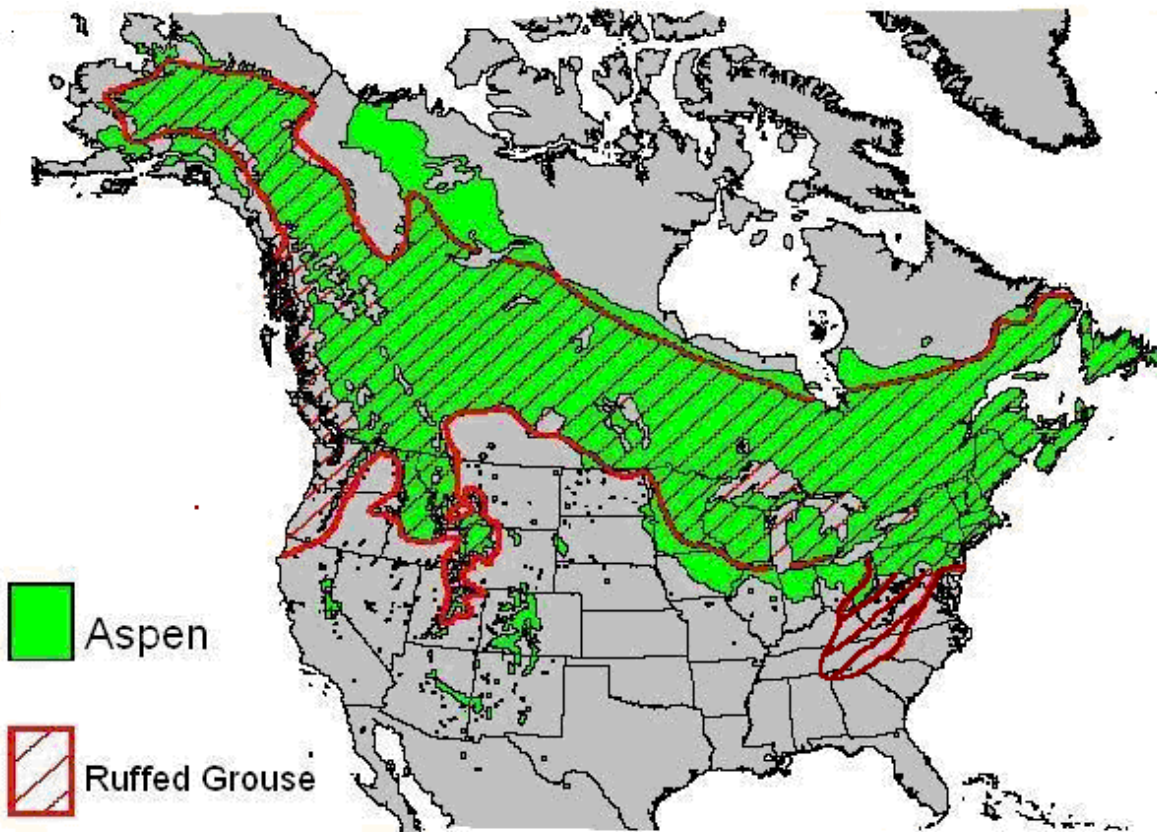


Figure 1. Distribution of ruffed grouse and aspen (*P. tremuloides*) in North America.

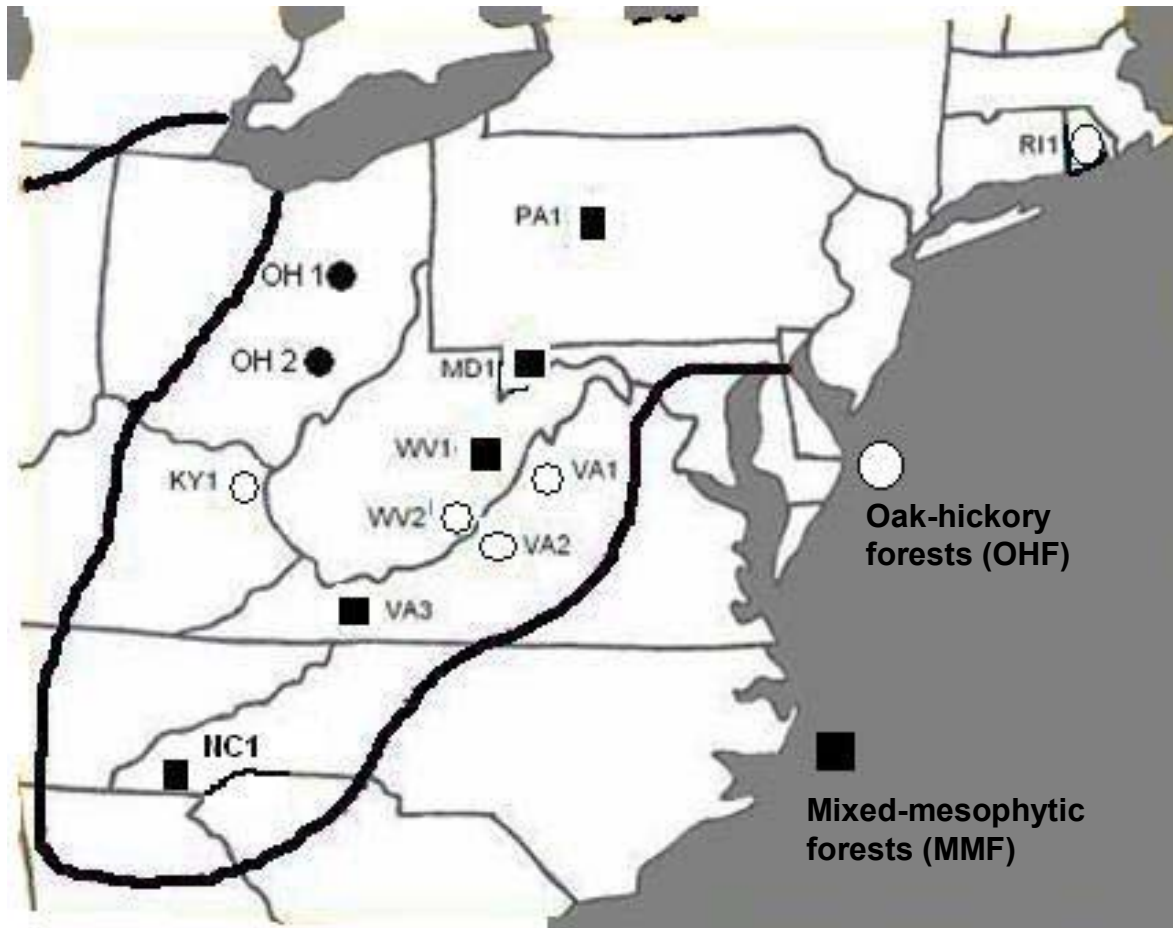


Figure 2. Location of Appalachian Cooperative Grouse Research Project study sites, 1996-2002. The heavy black line indicates the southern limits of the distribution of ruffed grouse in eastern North America. The OH1 and OH2 study areas were not classified to forest association due to the lack of data.

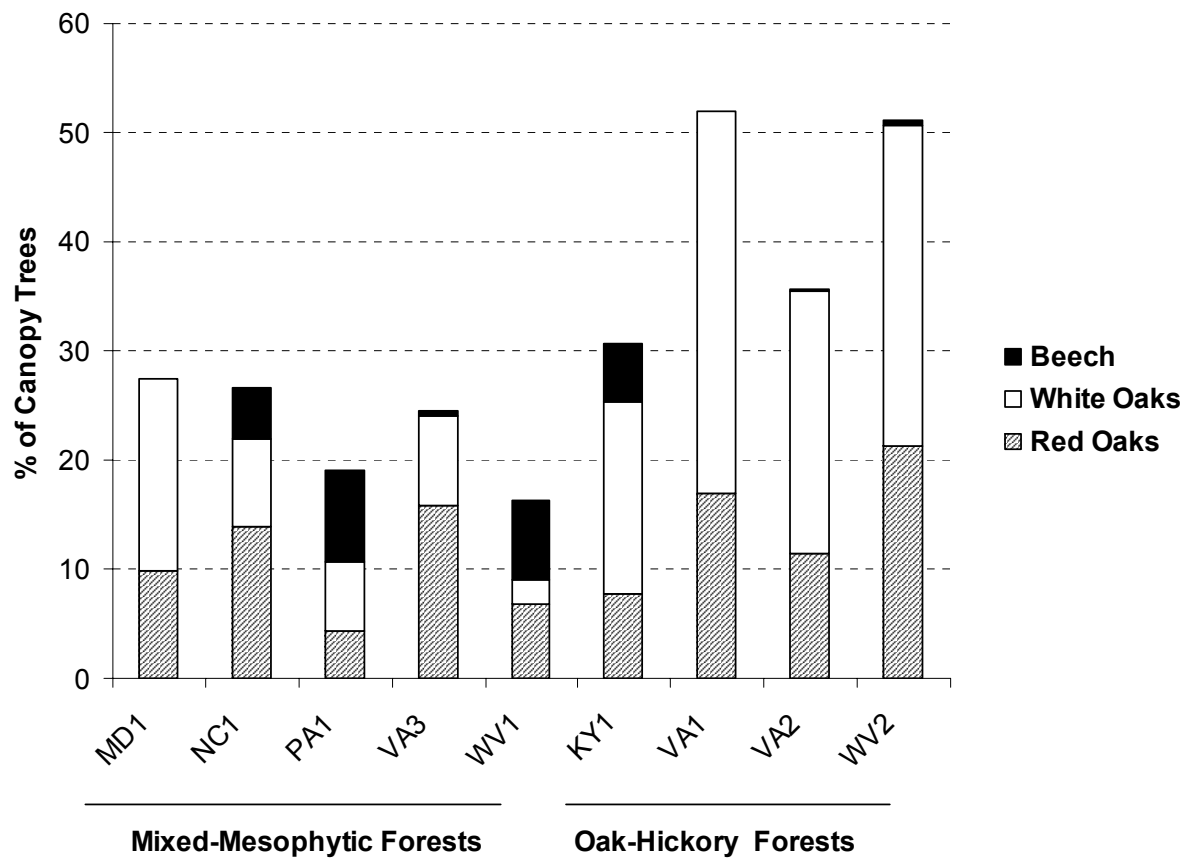


Figure 3. Percentage of canopy trees on ACGRP study sites represented by members of the red and white oak groups and beech. Data were collected at randomly located 0.04ha plots (J. Tirpak, Fordham University, unpublished data; D. Whitaker, Virginia Tech, unpublished data). Sample sizes varied across sites: MD1 (n=5,050), NC1 (n=5,587), PA1 (n=5,616), VA3 (n=7,259), WV1 (n=5,429), KY1 (n=3,825), VA1 (n=4,007), VA2 (n=6,142), and WV2 (n=7,804).

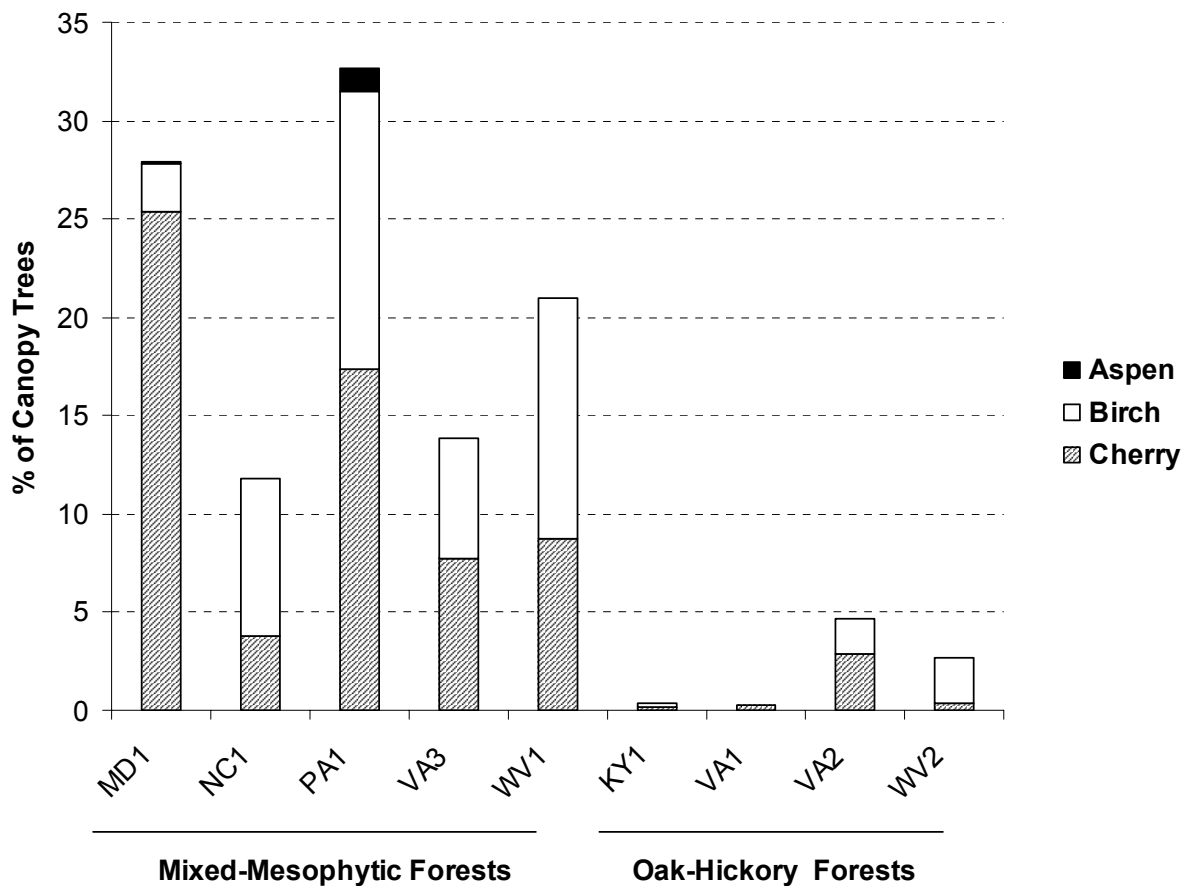


Figure 4. Percentage of canopy trees on ACGRP study sites represented by aspen, birch, and cherry. Data were collected at randomly located 0.04ha plots (J. Tirpak, Fordham University, unpublished data; D. Whitaker, Virginia Tech, unpublished data). Sample sizes varied across sites: MD1 (n=5,050), NC1 (n=5,587), PA1 (n=5,616), VA3 (n=7,259), WV1 (n=5,429), KY1 (n=3,825), VA1 (n=4,007), VA2 (n=6,142), and WV2 (n=7,804).

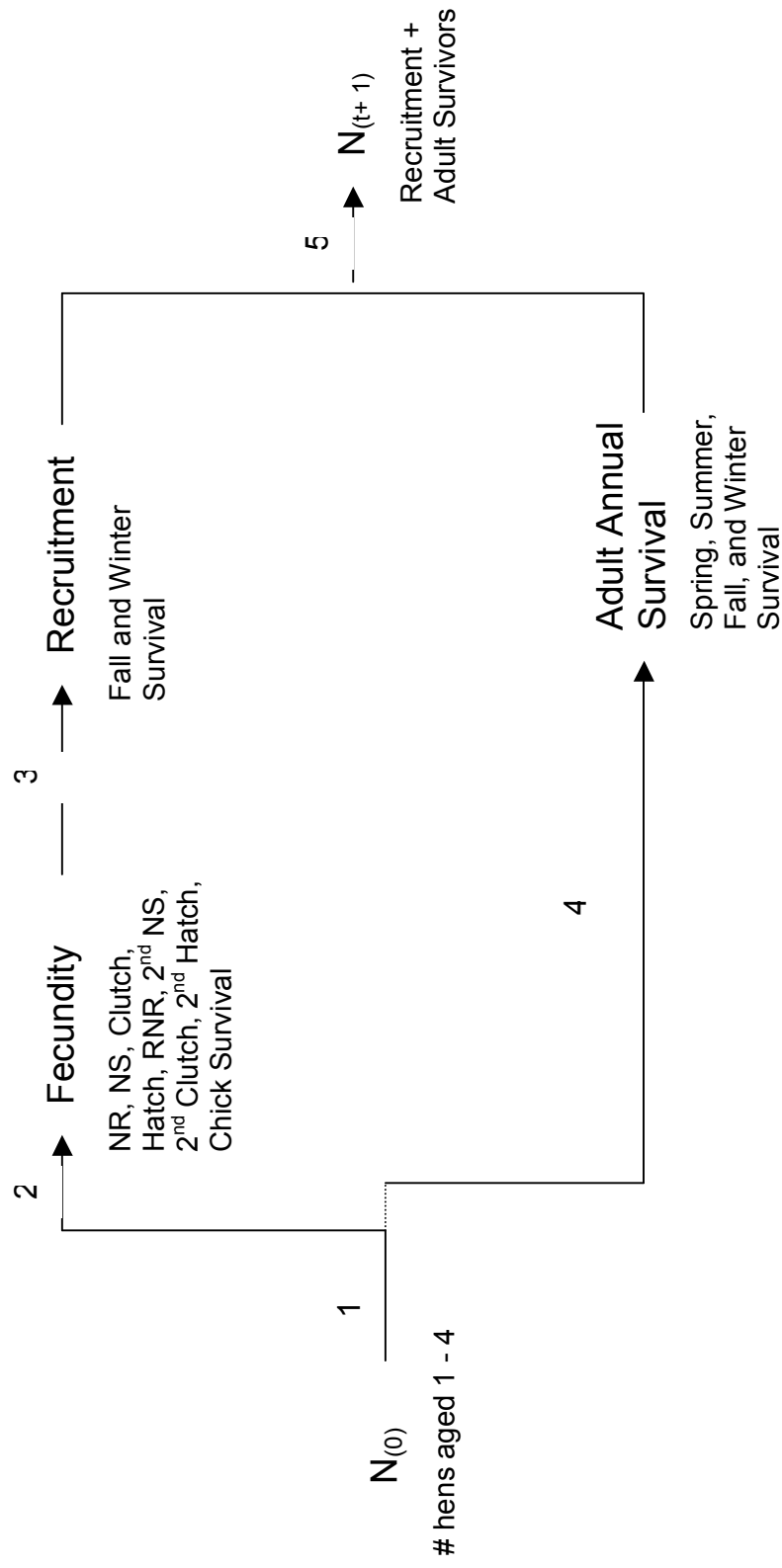


Figure 5. Schematic of modeling process for deterministic model 1.

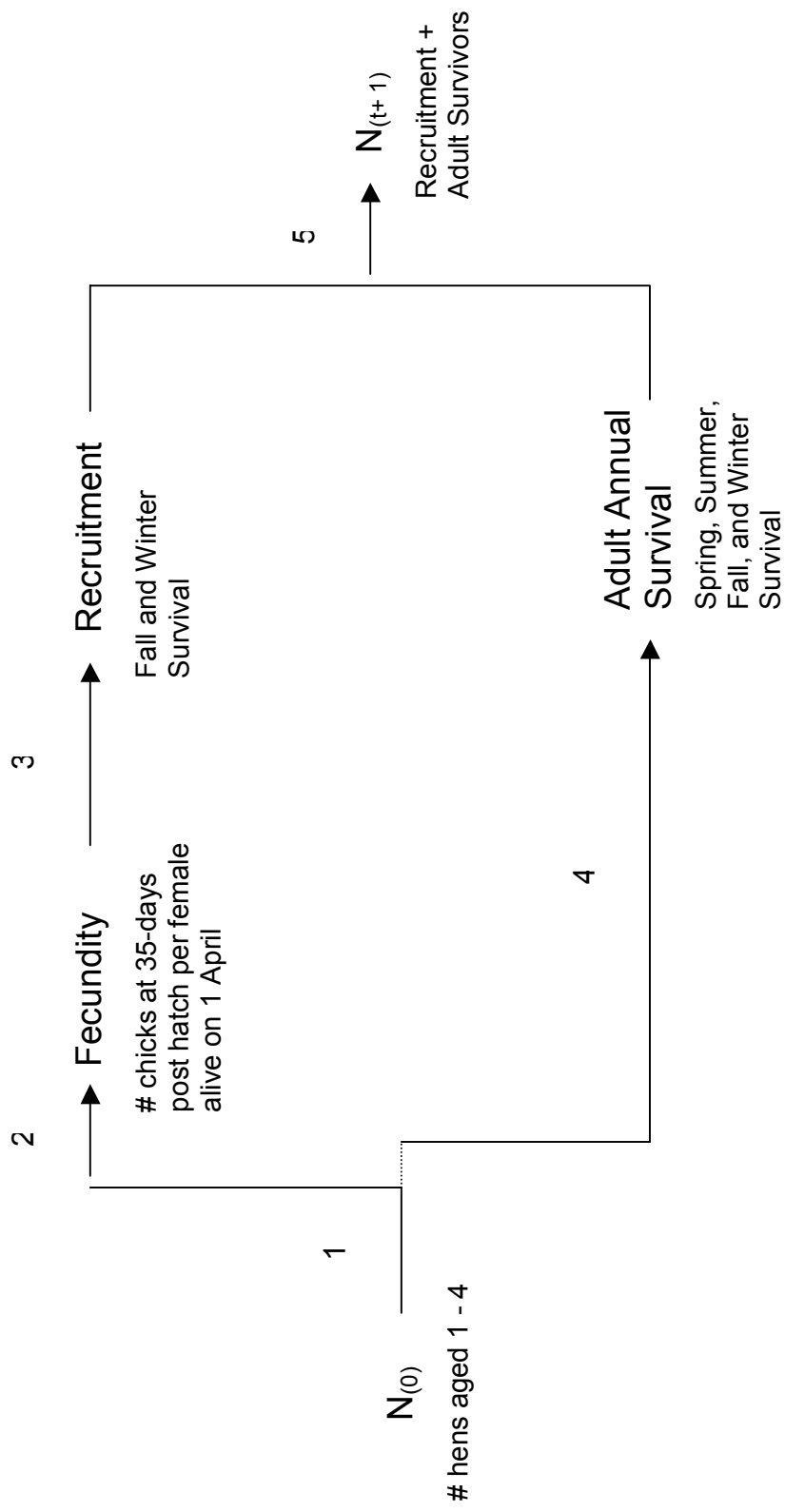


Figure 6. Schematic of modeling process for deterministic model 2 and stochastic model.

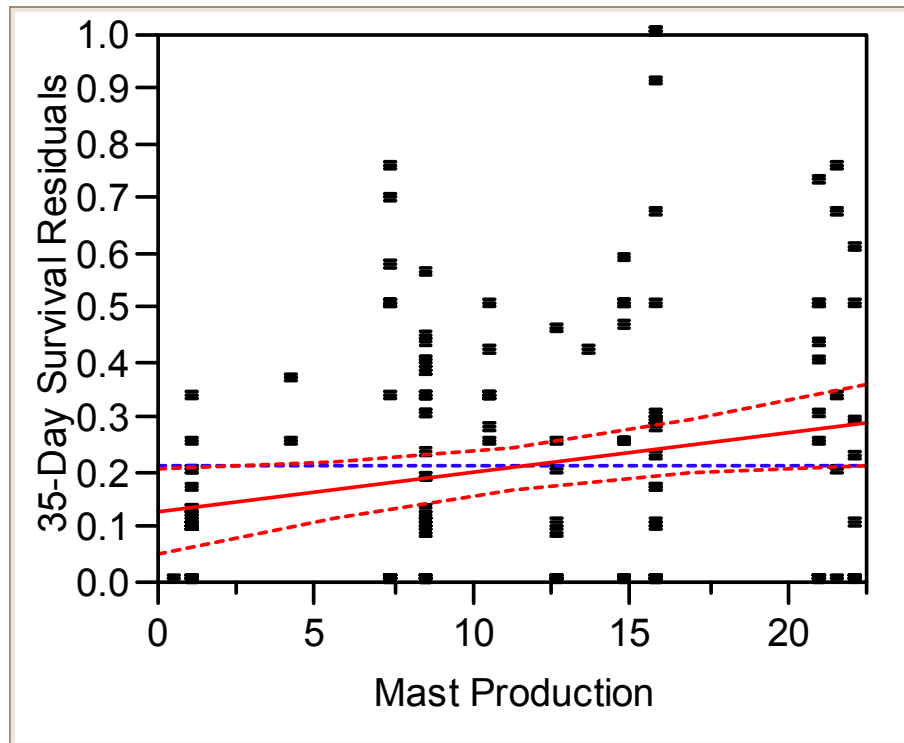


Figure 7. Relationship ($R^2 = 0.04$) between mast production the previous fall and ruffed grouse chick survival to 35-days post-hatch in the central Appalachian region, 1997 – 2002. Horizontal line indicates null hypothesis of no relationship. Remaining lines represent estimated slope and 95% confidence interval.

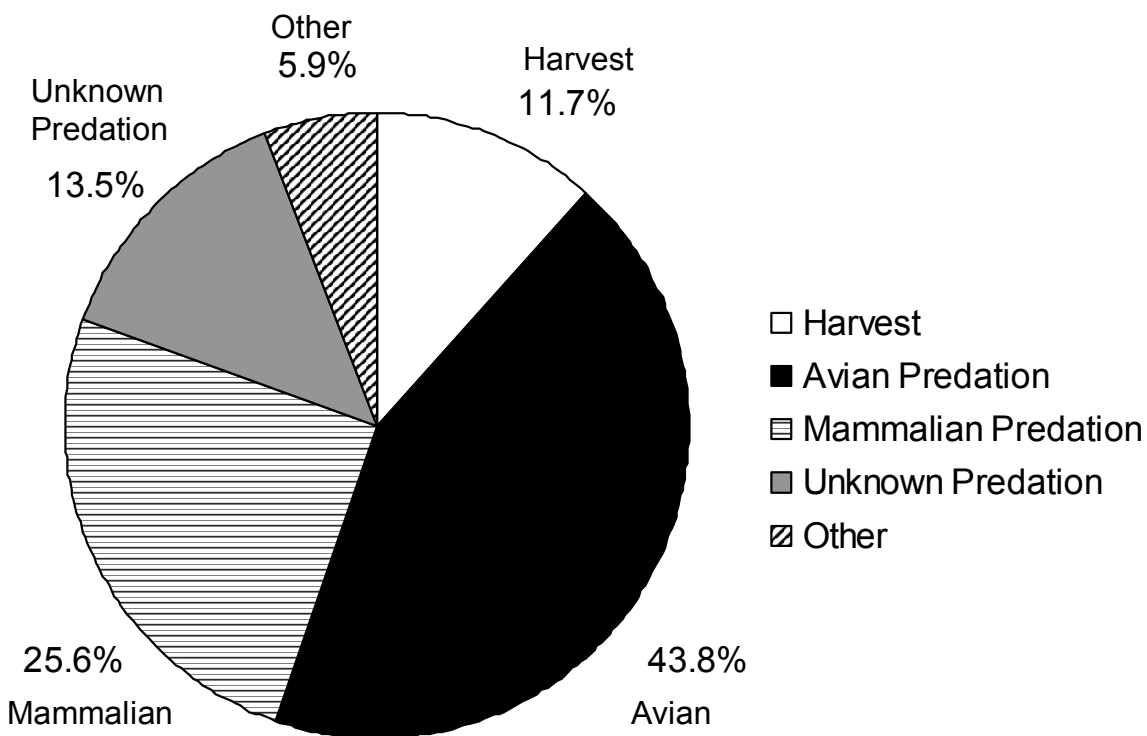


Figure 8. Percent of known ruffed grouse mortalities averaged across study areas and years ($n=45$) by cause in the southern and central Appalachian region, 1997 – 2002.

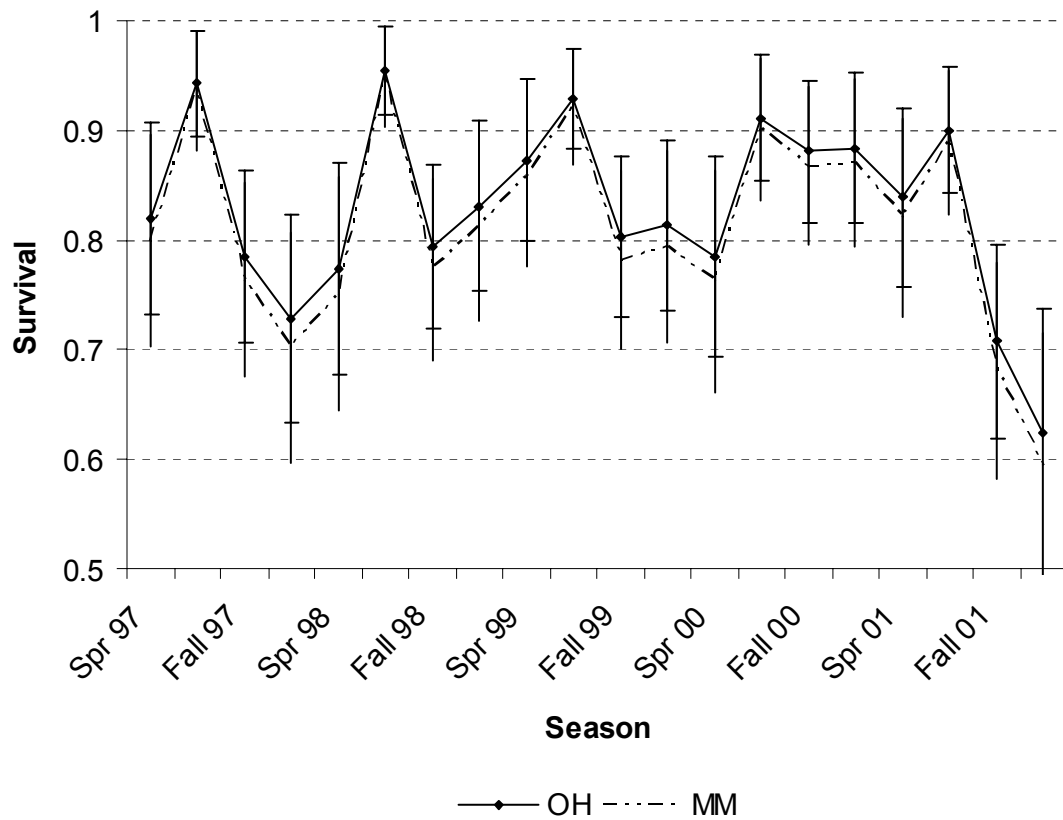


Figure 9. Ruffed grouse survival on oak-hickory (OH) and mixed-mesophytic (MM) forests in the southern and central Appalachian region, 1997 – 2002. Estimates were generated using the known-fates with covariates model in Program MARK.

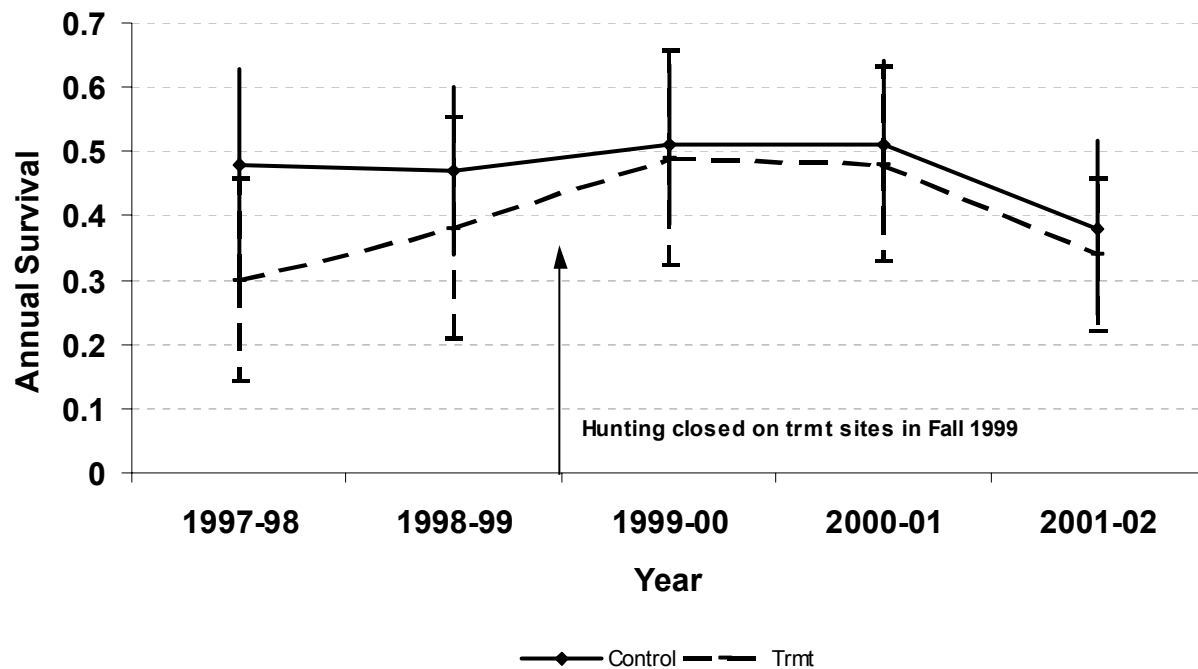


Figure 10. Ruffed grouse annual survival (pooled across sex and age class) on treatment and control sites in the southern and central Appalachian region, 1997 – 2002. Treatment sites were open to hunting from 1996 -1998 (Phase I) and closed to hunting from 1999 – 2001 (Phase II). Control sites were open to hunting every year. Estimates were obtained using the known-fates model in Program MARK.

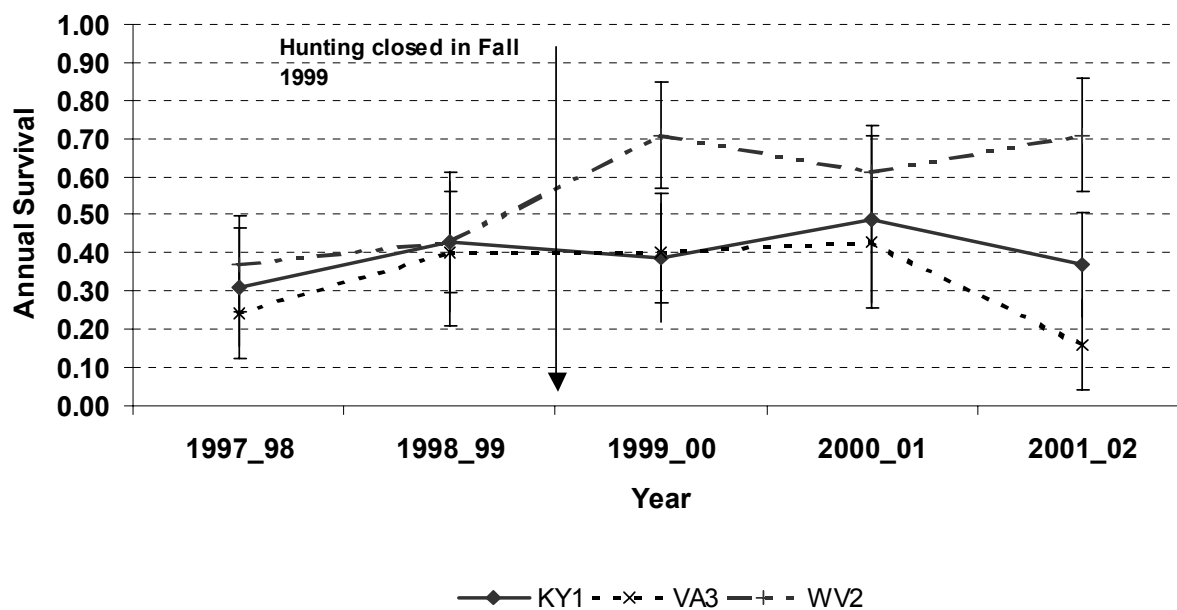


Figure 11. Ruffed grouse annual survival (pooled across sex and age class) on 3 treatment sites in the southern and central Appalachian region, 1997 – 2002.

Treatment sites were open to hunting from 1996 -1998 (Phase I) and closed to hunting from 1999 – 2001 (Phase II). Estimates were obtained using the known-fates model in Program MARK.

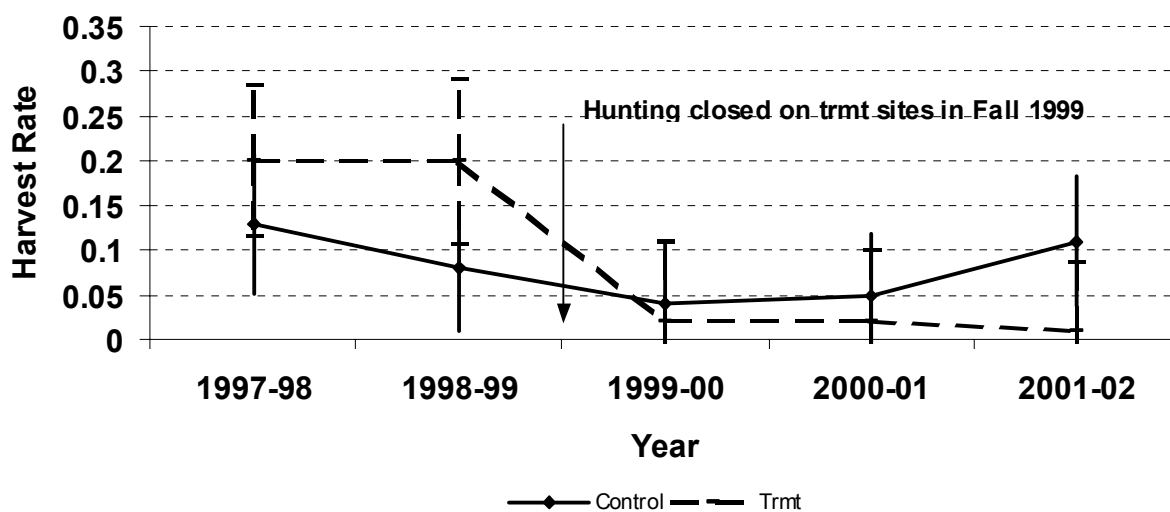


Figure 12. Ruffed grouse harvest rates on control and treatment sites in the southern and central Appalachian region, 1997 – 2002.

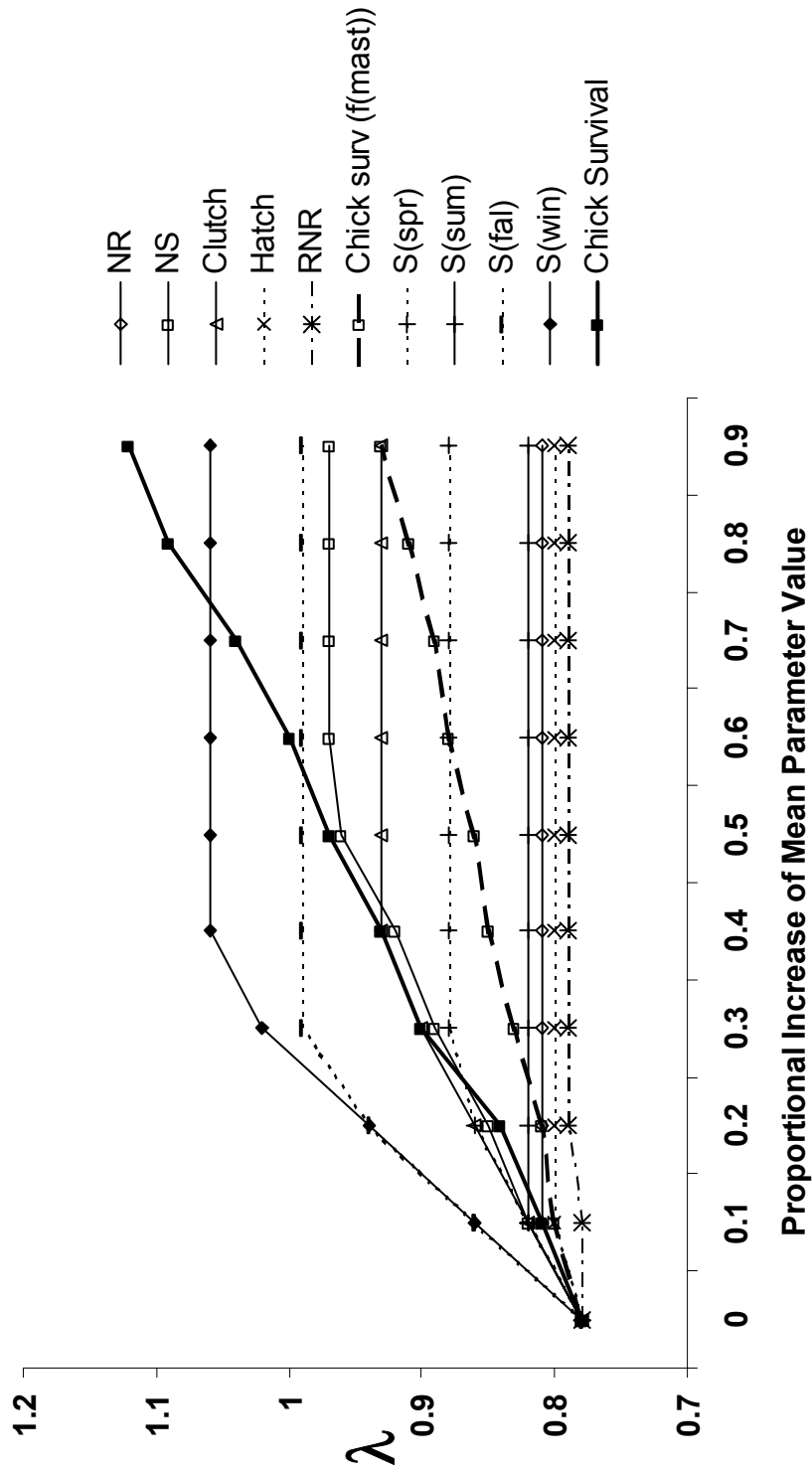


Figure 13. Elasticity analysis of ruffed grouse finite growth rate in the central Appalachian region based on Deterministic Model 1. This model used multiple parameters (i.e., nesting rate, nest success, clutch size, hatchability, etc.) to estimate productivity.

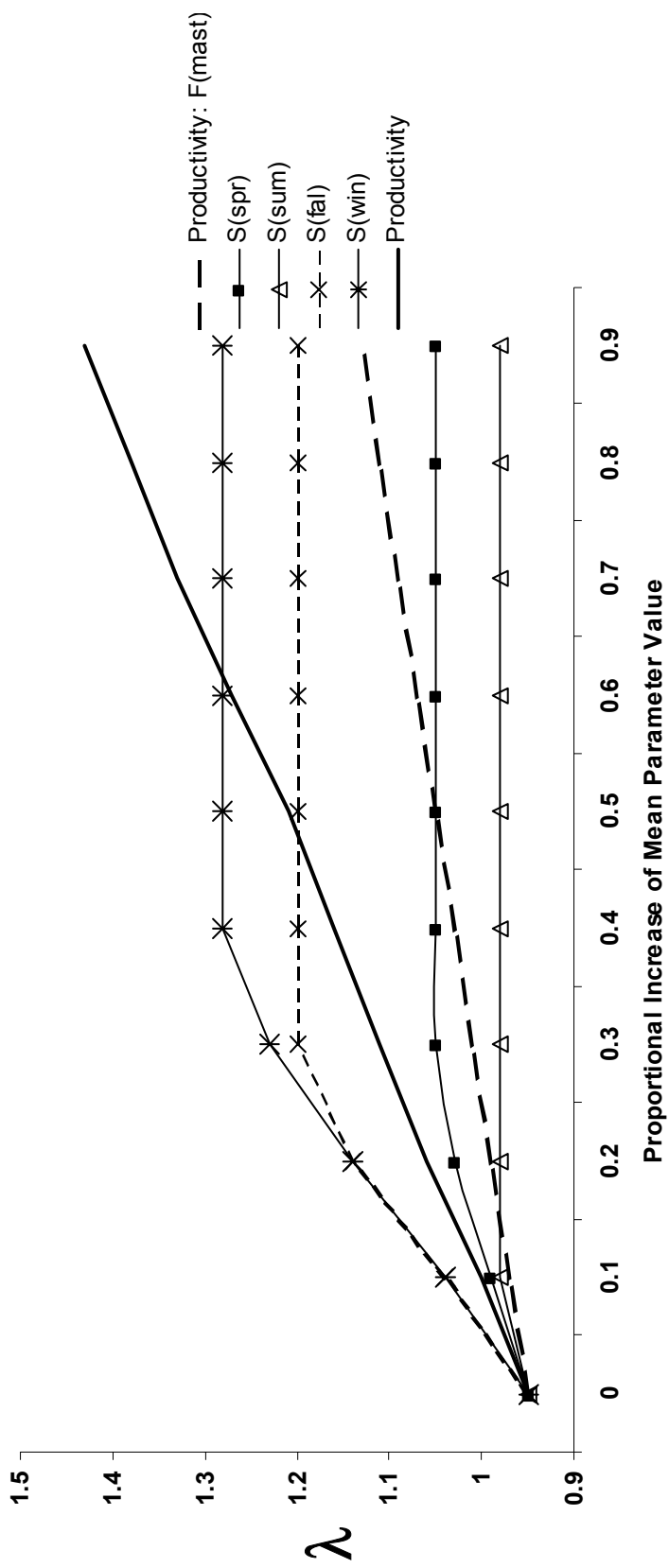


Figure 14. Elasticity analysis of ruffed grouse finite population growth rate in the central Appalachian region based on Model 2. Model 2 estimated productivity using 1 parameters (# chicks alive at 35 days post-hatch per female alive on 1 April).

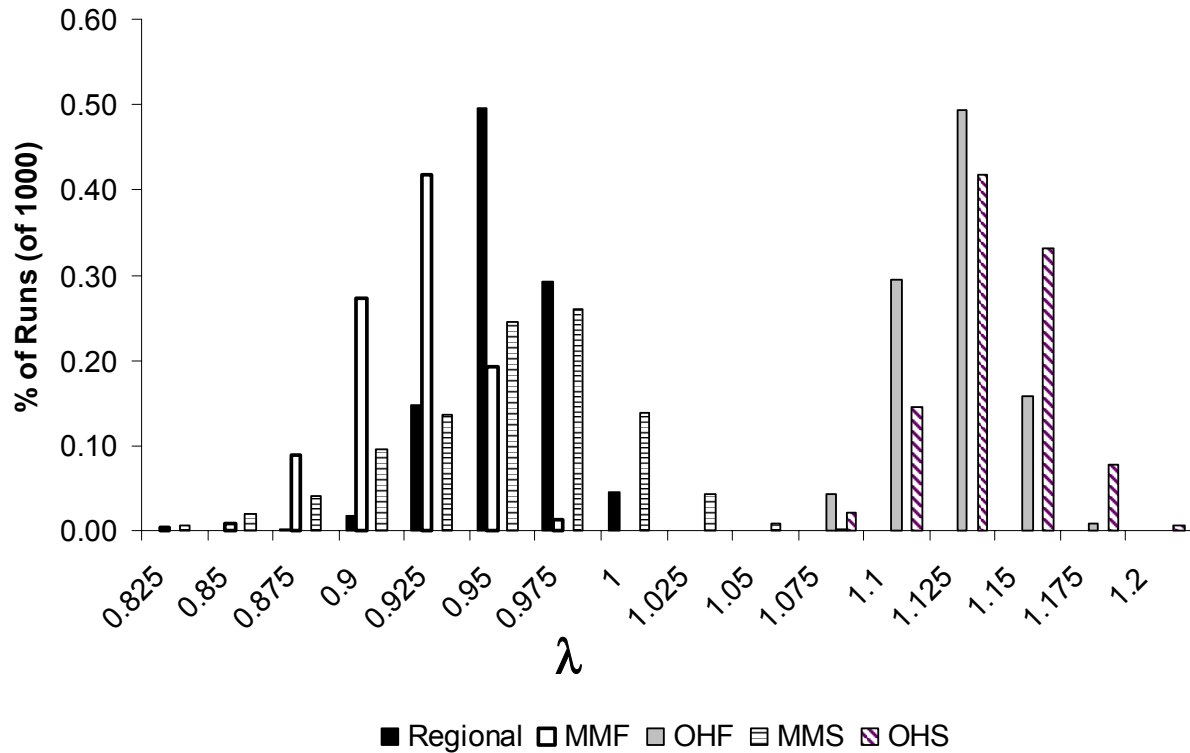


Figure 15. Distribution of estimated finite growth (λ) rates at 5 spatial scales in the central Appalachian region based on a stochastic population model. Parameter estimates at the regional scale were calculated by pooling across all study areas and averaging across years. Parameter estimates for mixed-mesophytic (MMF) and oak-hickory (OHF) forests were calculated by pooling across study areas identified as dominated by each respective forest association and averaged across years. Parameter estimates for mixed-mesophytic (MMS) and oak-hickory (OHS) forest study areas were calculated by averaging across years and study sites identified as dominated by each respective forest type.

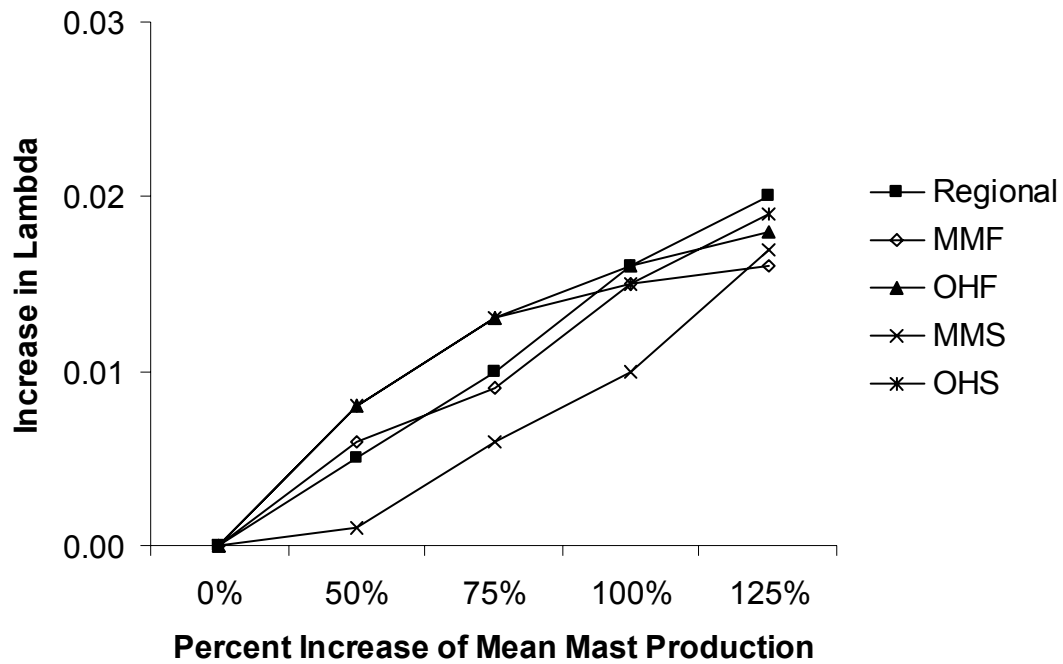


Figure 16. Estimated effects of increasing mean annual hard mast production on ruffed grouse finite population growth rate at multiple spatial scales in the southern and central Appalachian based a stochastic population model.

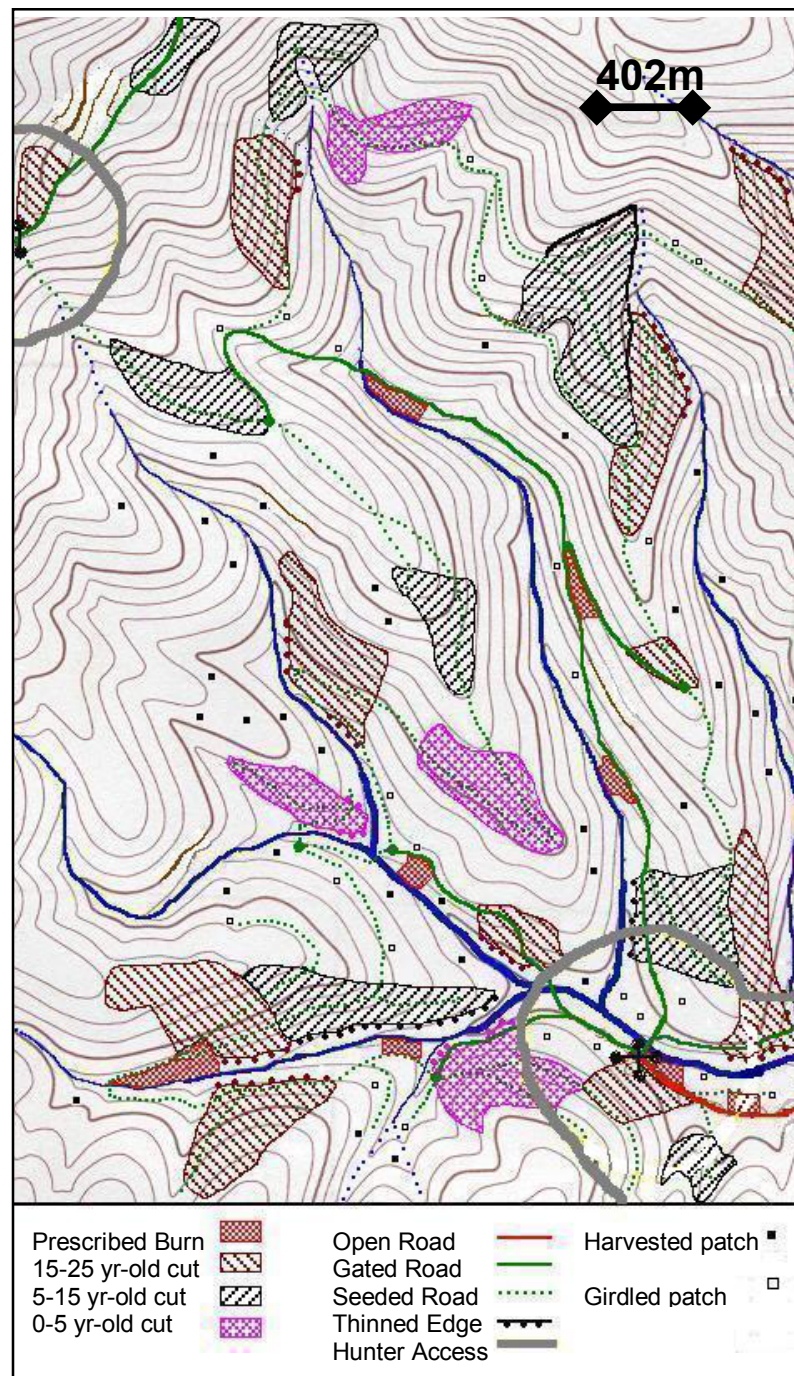


Figure 17. Hypothetical 205ha landscape (adopted from Whitaker 2003) with placement of gates emphasizing “refuge” areas for ruffed grouse over “recreational” areas for high quality hunting opportunities. Recreational areas are $\leq 402\text{m}$ from an open road and are outlined in gray.

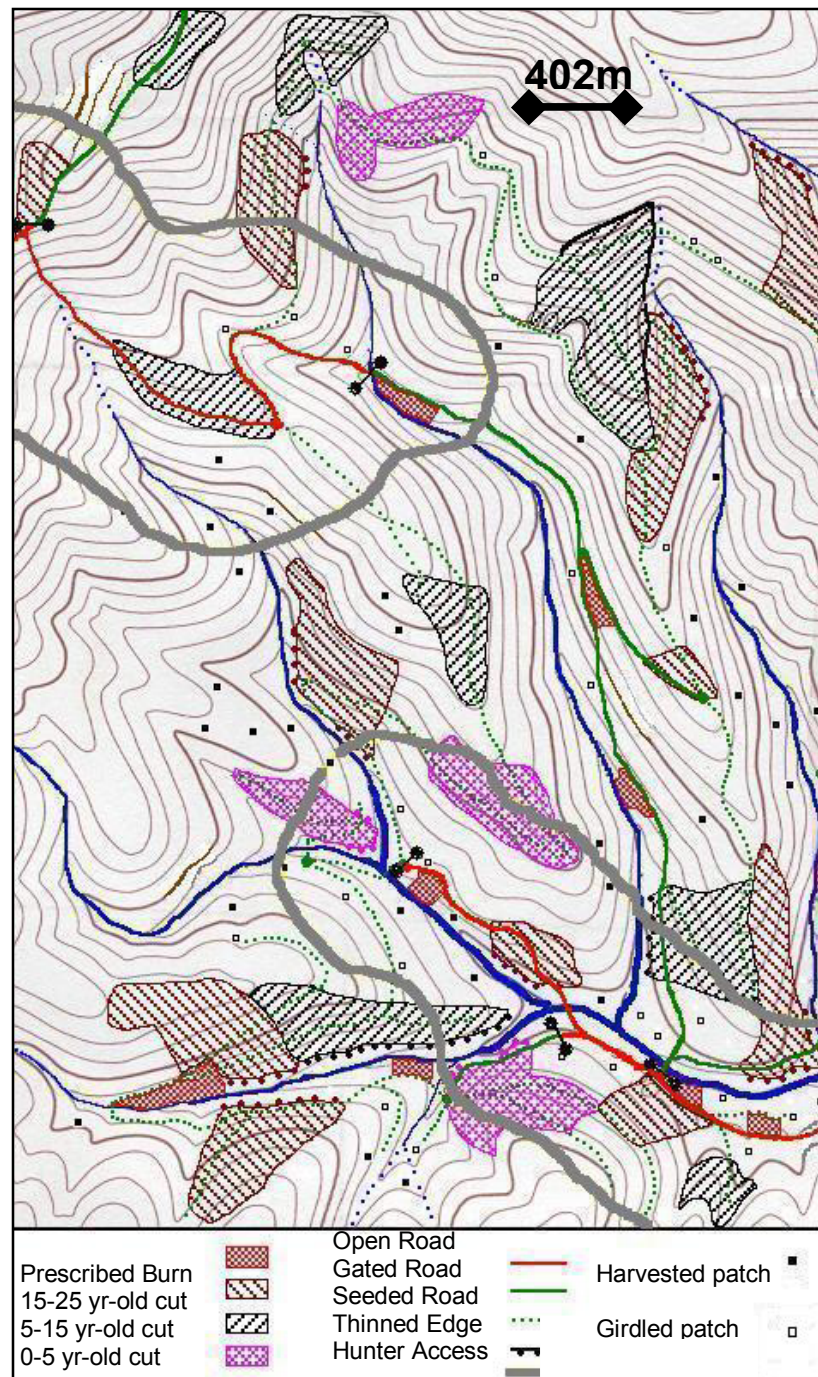


Figure 18. Hypothetical 205ha landscape (adopted from Whitaker 2003) with placement of gates emphasizing “recreational” areas for high quality hunting opportunities over “refuge” areas for ruffed grouse. Recreational areas are $\leq 402\text{m}$ from an open road and are outlined in gray.

APPENDIX A: Summary of site-specific mean reproductive and survival rates.

Table A1. Mean ruffed grouse nesting rates in the southern and central Appalachian region, 1997 - 2002. Estimates were calculated by averaging across individuals in each year and then taking an average across years. Sample size (n) refers to the number of years.

Site	n	\bar{x}	sd	95% CI
KY1	6	1.0	0.0	N/A
MD1	6	1.0	0.0	N/A
NC1	3	1.0	0.0	N/A
OH1	3	1.0	0.0	N/A
OH2	3	1.0	0.0	N/A
PA1	4	1.0	0.0	N/A
RI1	3	1.0	0.0	N/A
VA1	5	0.69	0.43	0.36 – 1.0
VA2	6	0.96	0.1	0.88 – 1.0
VA3	6	1.0	0.0	N/A
WV1	6	0.98	0.04	0.95 – 1.0
WV2	6	0.85	0.21	0.68 – 1.0

Table A2. Mean ruffed grouse incubation date in the southern and central Appalachian region, 1997 - 2002. Estimates were calculated by averaging across individuals in each year and then taking an average across years. Sample size (n) refers to the number of years.

Site	n	\bar{x}	sd	95% CI
KY1	6	22 Apr	3.83 days	19 Apr – 26 Apr
MD1	6	4 May	2.28 days	2 May – 6 May
NC1	3	27 Apr	3.51 days	23 Apr – 1 May
OH1	3	27 Apr	5.13 days	21 Apr – 2 May
OH2	3	23 Apr	1.73 days	21 Apr – 25 Apr
PA1	4	8 May	2.06 days	6 May – 10 May
RI1	3	10 May	4.58 days	5 May – 15 May
VA1	4	29 Apr	3.77 days	25 Apr – 2 May
VA2	6	27 Apr	2.93 days	24 Apr – 29 Apr
VA3	6	2 May	2.0 days	30 Apr – 4 May
WV1	6	2 May	3.97 days	29 Apr – 5 May
WV2	6	29 Apr	6.10 days	24 Apr – 5 May

Table A3. Mean ruffed grouse clutch size (of 1st nests) in the southern and central Appalachian region, 1997 - 2002. Estimates were calculated by averaging across individuals in each year and then taking an average across years. Sample size (*n*) refers to the number of years.

Site	n	\bar{x}	sd	95% CI
KY1	6	9.25	1.23	8.26 – 10.24
MD1	6	10.92	0.83	10.25 – 11.58
NC1	3	9.97	0.47	9.43 – 10.50
OH1	3	10.67	2.17	8.21 – 13.13
OH2	3	9.87	0.51	9.29 – 10.45
PA1	4	9.90	0.51	9.40 – 10.40
RI1	3	9.83	1.61	8.01 – 11.65
VA1	4	9.15	0.90	8.27 – 10.03
VA2	6	8.62	1.78	7.19 – 10.04
VA3	6	9.97	1.16	9.04 – 10.89
WV1	6	10.02	1.01	9.21 – 10.82
WV2	5	9.00	1.56	7.63 – 10.37

Table A4. Mean ruffed grouse nest success (of 1st nests) in the southern and central Appalachian region, 1997 - 2002. Estimates were calculated by averaging across individuals in each year and then taking an average across years. Sample size (*n*) refers to the number of years.

Site	n	\bar{x}	sd	95% CI
KY1	6	0.70	0.19	0.33 – 1.0
MD1	6	0.64	0.04	0.26 – 1.0
NC1	3	0.83	0.05	0.40 – 1.0
OH1	3	0.71	0.07	0.20 – 1.0
OH2	3	0.69	0.07	0.17 – 1.0
PA1	4	0.52	0.06	0.03 – 1.0
RI1	3	0.78	0.06	0.31 – 1.0
VA1	4	0.92	0.02	0.66 – 1.0
VA2	6	0.47	0.04	0.07 – 0.87
VA3	6	0.77	0.03	0.44 – 1.0
WV1	6	0.71	0.03	0.34 – 1.0
WV2	5	0.62	0.05	0.19 – 1.0

Table A5. Mean ruffed grouse re-nest rate in the southern and central Appalachian region, 1997 - 2002. Estimates were calculated by averaging across individuals in each year and then taking an average across years. Sample size (n) refers to the number of years.

Site	n	\bar{x}	sd	95% CI
KY1	3	0.5	0.08	0.0 – 1.0
MD1	5	0.37	0.05	0.0 – 0.80
NC1	2	0.25	0.09	0.0 – 0.85
OH1	2	0.0	0.0	N/A
OH2	2	1.0	0.0	N/A
PA1	4	0.33	0.06	0.0 – 0.79
RI1	1	0.5	N/A	N/A
VA1	2	0.0	0.0	N/A
VA2	5	0.0	0.0	N/A
VA3	3	0.12	0.03	0.0 – 0.48
WV1	6	0.38	0.04	0.0 – 0.77
WV2	4	0.05	0.01	0.0 – 0.26

Table A6. Mean ruffed grouse hatchability in the southern and central Appalachian region, 1997 - 2002. Estimates were calculated by averaging across individuals in each year and then taking an average across years. Sample size (n) refers to the number of years.

Site	n	\bar{x}	sd	95% CI
KY1	6	0.87	0.02	0.60 – 1.0
MD1	6	0.86	0.02	0.58 – 1.0
NC1	3	0.95	0.01	0.71 – 1.0
OH1	3	0.98	0.01	0.81 – 1.0
OH2	3	0.98	0.01	0.82 – 1.0
PA1	4	0.84	0.03	0.48 – 1.0
RI1	2	0.94	0.03	0.61 – 1.0
VA1	4	0.84	0.03	0.48 – 1.0
VA2	6	0.91	0.01	0.67 – 1.0
VA3	6	0.87	0.02	0.59 – 1.0
WV1	6	0.91	0.01	0.69 – 1.0
WV2	6	0.70	0.04	0.33 -1.0

Table A7. Mean ruffed grouse hen success in the southern and central Appalachian region, 1997 - 2002. Estimates were calculated by averaging across individuals in each year and then taking an average across years. Sample size (n) refers to the number of years.

Site	n	\bar{x}	sd	95% CI
KY1	6	0.78	0.03	0.45 – 1.0
MD1	6	0.67	0.04	0.30 – 1.0
NC1	3	0.83	0.05	0.40 – 1.0
OH1	3	0.71	0.07	0.20 – 1.0
OH2	3	0.81	0.05	0.36 – 1.0
PA1	4	0.58	0.06	0.09 – 1.0
RI1	3	0.89	0.03	0.54 – 1.0
VA1	4	0.92	0.02	0.66 – 1.0
VA2	6	0.47	0.04	0.07 – 0.87
VA3	6	0.77	0.03	0.44 – 1.0
WV1	6	0.74	0.03	0.38 – 1.0
WV2	5	0.65	0.05	0.24 – 1.0

Table A8. Mean ruffed grouse hen success in the southern and central Appalachian region, 1997 - 2002. Estimates were calculated by averaging across individuals in each year and then taking an average across years. Sample size (n) refers to the number of years.

Site	n	\bar{x}	sd	95% CI
KY1	6	0.19	0.03	0.0 – 0.50
MD1	6	0.32	0.04	0.0 – 0.70
NC1	2	0.22	0.08	0.0 – 0.78
OH1	3	0.47	0.08	0.0 – 1.0
OH2	2	0.27	0.1	0.0 – 0.89
PA1	4	0.32	0.05	0.0 – 0.77
RI1	2	0.04	0.02	0.0 – 0.31
VA1	4	0.22	0.04	0.0 – 0.62
VA2	6	0.16	0.02	0.0 – 0.45
VA3	6	0.16	0.02	0.0 – 0.44
WV1	6	0.13	0.02	0.0 – 0.39
WV2	5	0.30	0.04	0.0 – 0.71

Table A9. Mean ruffed grouse annual survival in the southern and central Appalachian region, 1997 - 2002. Estimates were calculated by averaging across individuals in each year and then taking an average across years. Sample size (n) refers to the number of years.

Site	n	\bar{x}	sd	95% CI
KY1	5	0.40	0.067	0.31 – 0.48
MD1	5	0.35	0.039	0.30 – 0.40
NC1	2	0.33	0.064	0.0 – 0.90
OH1	2	0.55	0.035	0.23 – 0.86
OH2	2	0.17	0.120	0.0 – 1.0
PA1	3	0.29	0.076	0.11 – 0.48
RI1	2	0.30	0.127	0.0 – 1.0
VA1	4	0.56	0.074	0.45 – 0.68
VA2	5	0.49	0.140	0.31 – 0.67
VA3	5	0.33	0.119	0.18 – 0.47
WV1	5	0.47	0.104	0.34 – 0.60
WV2	5	0.57	0.158	0.37 – 0.76

Vita

PATRICK K. DEVERS

RESEARCH INTEREST

My research interests include wildlife population dynamics and the human dimensions of wildlife conservation. My interests developed from a variety of field experiences that highlighted the intersection of these separate but equally important aspects of applied conservation. More recently, my interests have grown to include community and disturbance processes.

EDUCATION

PH. D., *Wildlife Science*, January 2005. Population ecology and the effects of hunting on ruffed grouse in the southern and central Appalachian region. Virginia Polytechnic Institute and State University (Virginia Tech), Blacksburg, VA USA.

Advisor: Dean F. Stauffer

M.S., *Renewable Natural Resources*, August 1999. *Public attitudes, wildlife, and recreation Management in Pusch Ridge Wilderness, Arizona, USA. The University of Arizona, Tucson, Arizona USA.*

Advisor: Paul R. Krausman

B.S., *Wildlife Biology*, May 1997. *Minor Range Ecology. Colorado State University, Fort Collins, Colorado, USA.*

HONORS

Donald H. Rusch Memorial Scholarship, The Wildlife Society	2002
Chamberline Fellowship, Virginia Tech	2002
Arizona Desert Bighorn Sheep Society Scholarship	1998, 1999
Meritorious Teaching Award, University of Arizona	1998
Associate Wildlife Biologist, The Wildlife Society	1997
Boone and Crockett Club Award, The Wildlife Society	1997