Ruffed Grouse Population Ecology in the Appalachian Region

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ABSTRACT The Appalachian Cooperative Grouse Research Project (ACGRP) was a multistate cooperative effort initiated in 1996 to investigate the apparent decline of ruffed grouse (*Bonasa umbellus*) and improve management throughout the central and southern Appalachian region (i.e., parts of Ohio, Pennsylvania, Rhode Island, Kentucky, West Virginia, Virginia, and North Carolina, USA). Researchers have offered several hypotheses to explain the low abundance of ruffed grouse in the region, including low availability of early-successional forests due to changes in land use, additive harvest mortality, low productivity and recruitment, and nutritional stress. As part of the ACGRP, we investigated ruffed grouse population ecology. Our objectives were to estimate reproductive rates, estimate survival and cause-specific mortality rates, examine if ruffed grouse harvest in the Appalachian region is compensatory, and estimate ruffed grouse finite population growth. We trapped >3,000 ruffed grouse in autumn (Sep–Nov) and spring (Feb–Mar) from 1996 to September 2002 on 12 study areas. We determined the age and gender of each bird and fitted them with necklace-style radiotransmitters and released them at the trap site. We tracked ruffed grouse ≥ 2 times per week using handheld radiotelemetry equipment and gathered data on reproduction, recruitment, survival, and mortality.

Ruffed grouse population dynamics in the Appalachian region differed from the central portion of the species' range (i.e., northern United States and Canada). Ruffed grouse in the Appalachian region had lower productivity and recruitment, but higher survival than reported for populations in the Great Lakes region and southern Canada. Population dynamics differed between oak (*Quercus* spp.)–hickory (*Carya* spp.) and mixed-mesophytic forest associations within the southern and central Appalachian region. 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 12% of all known mortalities and appeared to be compensatory. Population models indicated ruffed grouse populations in the Appalachian region are declining ($\lambda = 0.78$–0.95), but differences in model estimates highlighted the need for improved understanding of annual productivity and recruitment. We posit ruffed grouse in the Appalachian region exhibit a clinal population structure characterized by changes in life-history strategies. Changes in life history strategies are in response to gradual changes in forest structure, quality of food resources, snowfall and accumulation patterns, and predator communities. Management efforts should focus on creating a mosaic of forest stand ages across the landscape to intersperse habitat resources including nesting and brood cover, adult escape cover, roosting sites, and, most importantly, food resources. Land managers can intersperse habitat resources through a combination of clearcutting, shelterwood harvests, group selection, and timber stand improvement (including various thinnings and prescribed fire). Managers should maintain current ruffed grouse harvest rates while providing high quality hunting opportunities. We define high quality hunting as low hunting pressure, low vehicle traffic, and high flush rates. Managers can provide high quality hunting opportunities through use of road closures in conjunction with habitat management. (WILDLIFE MONOGRAPHS 168, 1–36)

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KEY WORDS Acorns, Appalachian Mountains, *Bonasa umbellus*, harvest, hunting, management, population ecology, reproduction, ruffed grouse, survival.

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Ecología Superada de la Población del Grouse en la Región Apalache

RESUMEN El proyecto de investigación cooperativo del grouse superado de apalache (ACGRP) era un esfuerzo cooperativo del multi-estado iniciado en 1996 para investigar la declinación evidente del grouse superado (*Bonasa umbellus*) y para mejorar el manejo a través de la región apalache central y meridional (es decir, partes de Ohio, de Pennsylvania, de Rhode Island, de Kentucky, de Virginia Occidental, de Virginia, y de Tennessee, en los E.E.U.U.). Como parte de la ACGRP, investigamos la ecología superada de la población del grouse superado. Nuestros objetivos eran: estimar las tarifas reproductivas, estimar la supervivencia y las tarifas causar-específicas de la mortalidad, examinar si la cosecha del grouse superado en la región apalache es compensatoria, y estimar el crecimiento finito superado de la población del grouse superado. Varias hipótesis se han ofrecido para explicar la abundancia baja del grouse superado en la región, incluyendo la disponibilidad baja de los bosques jóvenes debido a los cambios en utilización del suelo, mortalidad aditiva de la cosecha, bajo productividad y reclutamiento, y tensión alimenticia. Atrapamos grouse superado $>$3,000 en el otoño (septiembre a noviembre) y en la primavera (febrero a marzo) a partir de 1996 al septiembre de 2002 en 12 áreas del estudio. Determinamos la edad y el sexo de cada pájaro y los cupimos con los radio-transmisores del estilo collar y los lanzamos en el sitio de la trampa. Seguimos el grouse superado $\geq$2 veces por semana usando equipo de la telemetría de radio de la estilo de mano y recopilamos datos sobre la reproducción, el reclutamiento, la supervivencia, y la mortalidad.

La dinámica de población del grouse superado en la región apalache diferenció de la porción central alcance de la del especie (es decir, el norte de los Estados Unidos y Canadá). El grouse superado en la región apalache tenía una productividad y un reclutamiento más bajo, pero supervivencia más alta que divulgada para las poblaciones en la región de los Great Lakes y el Canadá meridional. La dinámica de población diferenció entre bosques del roble (*Quercus*), el nuez dura (*Carya*) y bosques del estilo mesophytic mezclado dentro de la región apalache meridional y central. La productividad y el reclutamiento eran más bajos en bosques del roble yel nuez dura, pero la supervivencia del adulto era más alta que en bosques mesophytic mezclados. Además, la productividad y reclutamiento del grouse superado fueron relacionados más fuertemente a la producción dura del mástil (es decir, bellota) en bosques del roble y nuez dura que en bosques mesophytic mezclado. La causa principal de la mortalidad del grouse superado era la depredación aviar (el 44% de mortalidades sabidas). La mortalidad de la cosecha explicó el 12% de todas las mortalidades sabidas y aparecía ser compensatoria. Los modelos de población indican que las poblaciones del grouse superado en la región apalache están declinando ($\lambda = 0.78$–0.95), pero las diferencias en las estimaciones modelo indican la necesidad de la comprensión mejorada de la productividad y del reclutamiento anuales. Postulamos que el grouse superado en la region apalache muestra una estructura de la población clinal con los cambios en estrategias de la vida-historia en respuesta a cambios graduales en la calidad de los recursos del alimento, las nevadas y los patrones de la acumulación, y las comunidades despredadoras. Los esfuerzos del manejo deben centrarse en crear un mosaico de las edades del soporte de bosque a través del paisaje para entremezclar recursos del habitat incluyendo la cubierta para nidos y la cría de jovenes, la cubierta del escape del adulto, sitios para perchas, y más importante recursos del alimento. Interspersion de los recursos del habitat se puede lograr con una combinación de cortes selectivos, de los cortes del claro, del fuego prescrito, y de crear boquetes de diámetro bajo del pabellón matando a árboles individuales. El manejo de la cosecha se debe diseñar para mantener tarifas actuales de la cosecha mientras que proporciona oportunidades de la caza de la alta calidad. Definimos la caza de la alta calidad como la presión baja de la caza, el tráfico bajo del vehículo, y tarifas rasantes del colmo. El manejo de la caza de la alta calidad puede ser lograda con el uso de los encierros del camino conjuntamente con el manejo del hábitat.

Écologie de Population de Grouse de Ruffed dans la Région Appalachienne

RÉSUMÉ Le projet de recherche coopératif appalachien (ACGRP) était un effort coopératif de multi-état lancé en 1996 pour étudier le déclin apparent de ruffed la grouse (*Bonasa umbellus*) et améliorent la gestion dans toute la région appalachienne centrale et méridionale (c.-à-d., régions de l'Ohio, de la Pennsylvanie, de Île de Rhode, du Kentucky, de la Virginie Occidentale, de la Virginie, et du Tennessee, Etats-Unis). En tant qu'élément de l'ACGRP, nous avons étudié ruffed l'écologie de population de grouse. Nos objectifs étaient : estimer les taux reproducteurs, estimer la survie et les taux causer-spécifiques de mortalité, les examiner si ruffed la grouse que la moisson dans la région appalachienne est compensatoire, et l'évaluation ruffed la croissance finie de population de grouse. Plusieurs hypothèses ont été offertes pour expliquer la basse abondance de ruffed la grouse dans la région, y compris la basse disponibilité des forêts d'early-successional dues aux changements de l'utilisation de la terre, la mortalité additive de moisson, la productivité et le recrutement faible, et l'effort alimentaire. Nous avons emprisonné $>$3,000 ruffed la grouse en automne (Septembre.–Nov.) et ressort (Fév.–Mars.) de 1996 au Septembre 2002 sur 12 secteurs d'étude. Nous avons déterminé l'âge et le sexe de chaque oiseau et les avons équipés des émetteurs par radio de collier-modèle et les avons libérés à l'emplacement de piège. Nous avons dépisté ruffed des temps de la grouse $\geq$2 par semaine à l'aide de l'équipement tenu dans la main de radiotélémétrie et avons recueilli des données sur la reproduction, le recrutement, la survie, et la mortalité.

La dynamique de population de grouse de Ruffed dans la région appalachienne a différé de la partie centrale de la gamme des espèces (c.-à-d., les Etats-Unis et le Canada nordiques). La grouse de Ruffed dans la région appalachienne a eu une productivité et un recrutement plus faible, mais une survie plus élevée que rapportée aux populations la région de Great Lakes et au Canada méridional. La dynamique de population a différé entre le chêne (*quercus*)–hickory (*Carya*) et associations mélangées-mesophytic de forêt dans la région appalachienne méridionale et centrale. La productivité et le recrutement étaient inférieurs dans des forêts de chêne-hickory, mais la survie d'adulte était plus haute que dans les forêts mélangées-mesophytic. En outre, ruffed la productivité de grouse et le recrutement plus fortement ont été liés à la production dure de mât (c.-à-d., gland) dans des forêts de chêne-hickory que dans les forêts mélangées-mesophytic. La principale cause de ruffed la grouse que la mortalité était la prédation aviaire (44% de mortalités connues). La mortalité de moisson a expliqué 12% de toutes les mortalités connues et a semblé être compensatoire. La population que les modèles indiquent ruffed la grouse les populations dans la région appalachienne refusent ($\lambda = 0.78$–0.95), mais les différences dans les évaluations modèles indiquent le besoin d'arrangement amélioré de la productivité et du recrutement annuels. Nous posons en principe ruffed la grouse dans l'objet exposé appalachien de région une structure de population de clinal avec des changements des stratégies de vie-histoire en réponse aux changements progressifs de la qualité des ressources de nourriture, des chutes de neige et des modèles d'accumulation, et des communautés prédatrices. Les efforts de gestion devraient se concentrer sur créer une mosaïque des âges de peuplement de forêt à travers le paysage pour entremêler des ressources d'habitat comprenant la couverture d'emboîtement et de couvée, la couverture d'évasion d'adulte, les emplacements roosting, et d'une manière plus importante les ressources de nourriture. Interspersion des ressources d'habitat peut être accompli par une combinaison des coupes sélectives, des coupes d'espace libre, du feu prescrit, et de créer des lacunes de faible diamètre de verrière en tuant différents arbres. La gestion de moisson devrait être conçue pour maintenir des taux courants de moisson tout en fournissant des occasions de chasse de qualité. Nous définissons la chasse de qualité en tant que la basse pression de chasse, le bas trafic de véhicule, et taux affleurants de haute. La gestion de chasse à qualité peut être accomplie par l'utilisation des fermetures de route en même temps que la gestion d'habitat.

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INTRODUCTION

The ruffed grouse is a popular gamebird distributed from Alaska across central and southern Canada and the northern United States to the Atlantic Coast, and southward into the central Rocky Mountains and Appalachian Mountains. Its distribution coincides closely with that of aspen (*Populus tremuloides, P. grandidentata*), except in the central and southern Appalachians where aspen is rare or nonexistent (Fig. 1). Current knowledge of ruffed grouse ecology and management is based primarily on research conducted in the northern United States and Canada (Bump et al. 1947; Dorney and Kabat 1960; Gullion and Marshall 1968; Gullion 1970, 1984). Prior to the initiation of the Appalachian Cooperative Grouse Research Project (ACGRP), there was a paucity of knowledge of ruffed grouse ecology and trends in the Appalachian region (Hein 1970, Rusch et al. 2000). Data collected as part of the United States Geological Survey Breeding Bird Survey show a -5.0% population change per year ($P = 0.05$, $n = 56$ routes; Sauer et al. 2004) in ruffed grouse population indices in the Appalachians over the last 3 decades.

Across their range, ruffed grouse prefer early-successional deciduous forests with high woody stem densities, dense woody cover, and dense herbaceous understory (Bump et al. 1947, White and Dimmick 1978, Johnsgard 1983, Kubisiak 1985, Thompson et al. 1987). In contrast to these broad generalizations, differences exist between grouse habitat and environmental conditions in the central portion of the species' range and the Appalachian region.

In the central portion of ruffed grouse range, aspen provides cover and food and is the most important component of ruffed grouse habitat. In the central range, young aspen stands with 14,000–20,000 stems/ha provide optimal drumming and winter cover (Thompson and Fritzell 1988). Aspen stands also commonly have moderately dense shrub and herbaceous layers that provide high quality brood cover (Svoboda and Gullion 1972). Aspen is an important food source for ruffed grouse, particularly during winter and prebreeding periods (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

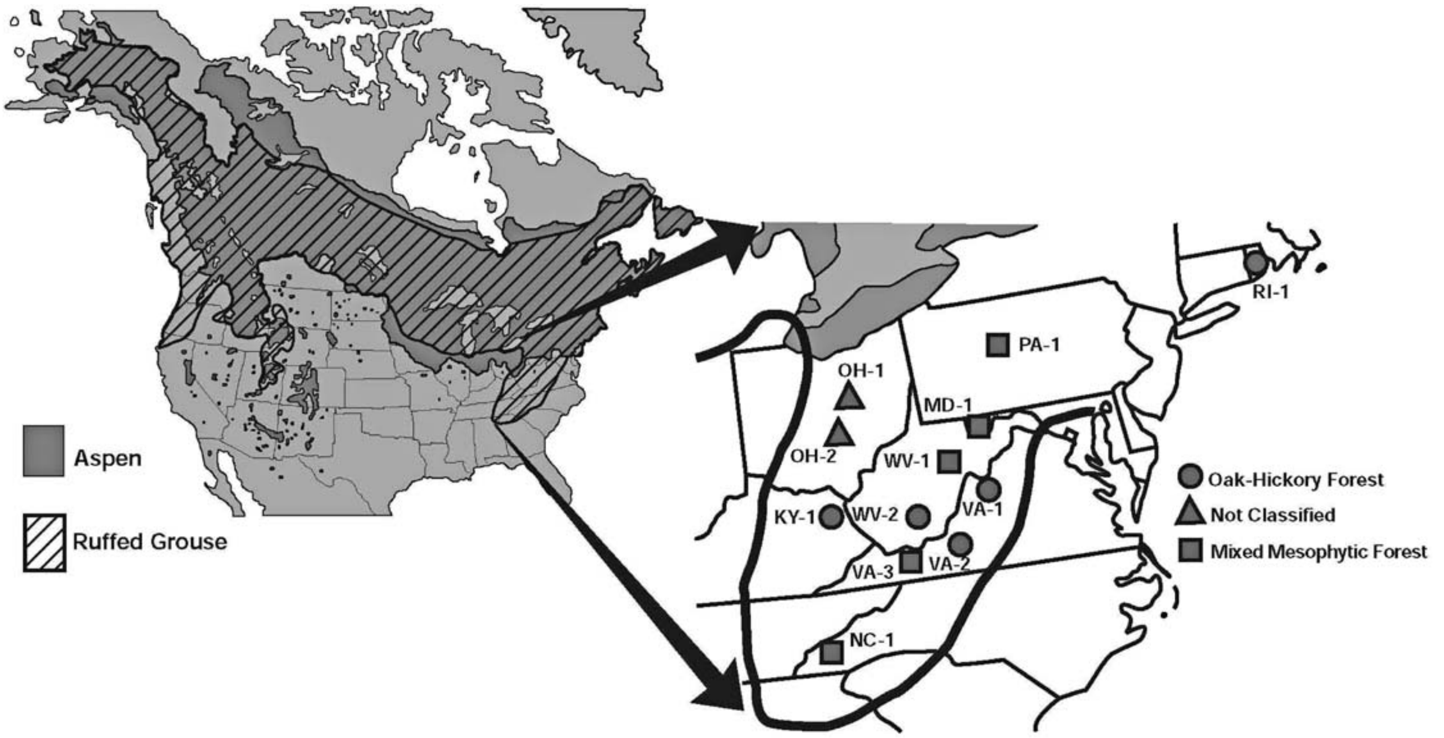

Figure 1. Distribution of ruffed grouse, aspen, and the locations of study areas in the southern and central Appalachian region, USA, 1996–2002. The heavy black line indicates the southern limits of the distribution of ruffed grouse in eastern North America. The OH-1 and OH-2 study areas were not classified to forest association due to the lack of data.

Appalachian region may provide less protection from raptors (Hein 1970) and lower quality forage (i.e., lower protein and higher levels of tannins; Servello and Kirkpatrick 1987) than aspen-dominated stands of the northern United States and Canada.

Availability and quality of food resources influence multiple aspects of avian reproduction and recruitment including clutch size, egg quality, incubation date, and chick survival (Williams 1994, Nager et al. 2000, Reynolds et al. 2003, Verboven et al. 2003). The nutritional quality of ruffed grouse diets differs markedly between the central range and Appalachian region. Throughout most of their range, ruffed grouse depend on aspen (i.e., buds, twigs, and catkins) to meet their winter nutritional requirements (Svoboda and Gullion 1972, Servello and Kirkpatrick 1987, Hewitt and Kirkpatrick 1996). Winter diets in the Appalachian region consist of leaves and seeds of herbaceous plants and evergreen species including mountain laurel and great rhododendron (*R. maximum*). Other food items include buds and nuts of oaks, beech (*Fagus grandifolia*), birch (*Betula* spp.), and cherry trees (*Prunus* spp.), 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 diets in the northern United States and Canada (Servello and Kirkpatrick 1987). The poor nutritional quality of ruffed grouse diets in the Appalachian region may result in increased foraging time and risk of predation, and decreased body condition, reproductive potential, and chick survival (Beckerton and Middleton 1982, Servello and Kirkpatrick 1987, Hewitt and Kirkpatrick 1996).

Harvest of ruffed grouse is based on general assumptions about upland game populations: 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). In the Appalachian region, ruffed grouse hunting seasons are longer than in the northern United States and Canada, and the majority of harvest is suspected to occur during late November to February (G. W. Norman, Virginia Department of Game and Inland Fisheries, personal communication). Concerns over the effects of late-season hunting on ruffed grouse populations (Fischer and Keith 1974, Gullion and Evans 1982) and equivocal results from field studies (Gullion and Marshall 1968, Kubisiak 1984, DeStefano and Rusch 1986, Baines and Linden 1991, Small et al. 1991) have raised a debate of these principles. Further, the compensatory mortality hypothesis has not been tested experimentally (Gullion 1984, Myrberget 1985, Baines and Linden 1991, Ellison 1991, Strickland et al. 1994).

To successfully manage ruffed grouse populations in the Appalachian region, managers must have an understanding of population trends, limiting factors (Leopold 1933), and the impact of harvest mortality. Our goals were to assess ruffed grouse population dynamics, identify limiting factors, and provide recommendations for ruffed grouse management in the Appalachian region. To meet our goals we established 4 objectives:

1. Estimate reproductive rates and identify factors that influence ruffed grouse reproduction.

Table 1. Description of study areas for the Appalachian Cooperative Grouse Research Project, 1996–2002.

Site	Ownership	Easting	Northing	RPI[a]	Forest type[b]	Treatment[c]	Yr
KY-1	State	345043	4215070	8.21	Oak–hickory	Closed	1996–2002
MD-1	State	650357	4224141	33.62	Mixed-mesophytic	Open	1996–2002
NC-1	Federal	263921	3896915	32.4	Mixed-mesophytic	N/A	1999–2002
OH-1	State, private	412219	4451653	N/A	N/A	N/A	1996–1999
OH-2	State, private	435700	1738000	N/A	N/A	N/A	1996–1999
PA-1	State	718089	4566156	35.96	Mixed-mesophytic	N/A	1998–2002
RI-1	State	271441	4608252	25.54	Oak–hickory	N/A	1999–2002
VA-1	Federal	650357	4224141	25.0	Oak–hickory	Open	1997–2002
VA-2	MeadWestvaco	614445	4168715	27.81	Oak–hickory	Open	1996–2002
VA-3	State	427140	4088102	33.13	Mixed-mesophytic	Closed	1996–2002
WV-1	MeadWestvaco	581316	4284707	34.73	Mixed-mesophytic	Open	1996–2002
WV-2	MeadWestvaco	562234	4190564	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 (1938) bioclimatic rule. 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. M. Tirpak, Fordham University, unpublished data), literature review (Braun 1950), and RPI.

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

2. Estimate survival and cause-specific mortality rates and identify factors that influence ruffed grouse survival.
3. Examine if ruffed grouse harvest in the Appalachian region is additive or compensatory.
4. Estimate ruffed grouse finite population growth rate in the Appalachian region.

STUDY AREA

We studied ruffed grouse populations on 12 sites in 8 states throughout the Appalachian region (Table 1, Fig. 1). Land ownership varied across sites and included National Forest land, state public land, private land, and industrial forest land owned by MeadWestvaco Corporation. Study areas ranged from 2,000 ha to 11,000 ha. The proportion of forest age classes (i.e., 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 the greatest proportion of sapling-age stands.

Study areas (except OH-1 and OH-2) were classified as oak–hickory or mixed-mesophytic forest associations based on Braun (1950), canopy tree composition and abundance data (J. M. Tirpak, Fordham University, unpublished data), and a relative phenology index (RPI; S. D. Klopfer, The Conservation Management Institute, unpublished data; Table 1, Fig. 1). 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 based on the mean latitude, longitude, and elevation of ruffed grouse radiotelemetry locations by year (1996–2001) and then averaged across years. The RPI values calculated for each study area indicated growing seasons on mixed-mesophytic sites (i.e., higher RPI values) were shorter than on oak–hickory sites despite the interspersion of the 2 forest associations in the Appalachian region (Fig. 1). We did not classify the OH-1 and OH-2 study areas 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 mixed-mesophytic 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. Hard mast producing species, including members of the red and white oak groups and beech, were present on mixed-mesophytic and oak–hickory forests but were more abundant on the latter (Fig. 2). Aspen, birch, and cherry, which provide high-quality foods for grouse, were more abundant on the former (Fig. 3). Scientific names follow United States Department of Agriculture Natural Resources Conservation Service PLANTS database convention (United States Department of Agriculture Natural Resources Conservation Service 2006).

In addition to the major differences in dominant forest associations, study sites also varied in topography, weather, species composition, and harvest regulations. Topographic relief was greatest on the Virginia, West Virginia, and North Carolina sites. The Rhode Island, Maryland, and Pennsylvania sites had the least variation in topographic relief. Monthly mean temperatures ranged from 8.1° C to 13.7° C across study sites (Bumann 2002). Snow cover was more common on the more northerly sites than on more southerly sites (Bumann 2002). Indices of predator species abundance (0.02–0.11 predators seen/hr), white-tailed deer (*Odocoileus virginianus*; 0.03–1.34 seen/hr), wild turkey (*Meleagris gallopavo*; 0.03–0.78 seen/hr), and alternative prey species (0.01–

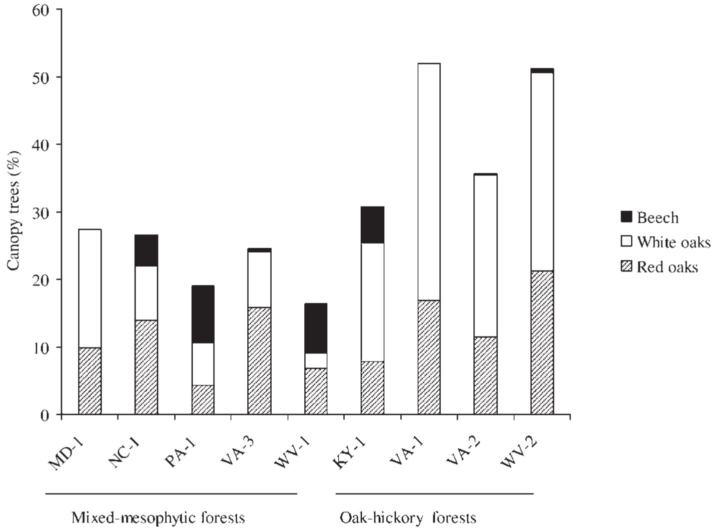

Figure 2. Percentage of canopy trees on Appalachian Cooperative Grouse Research Project study areas represented by members of the red and white oak groups and beech. Data were collected at randomly located 0.04-ha plots (J. M. Tirpak, Fordham University, unpublished data; D. M. Whitaker, Virginia Polytechnic Institute and State University, unpublished data). Sample sizes varied across sites: MD-1 (*n* = 5,050), NC-1 (*n* = 5,587), PA-1 (*n* = 5,616), VA-3 (*n* = 7,259), WV-1 (*n* = 5,429), KY-1 (*n* = 3,825), VA-1 (*n* = 4,007), VA-2 (*n* = 6,142), and WV-2 (*n* = 7,804).

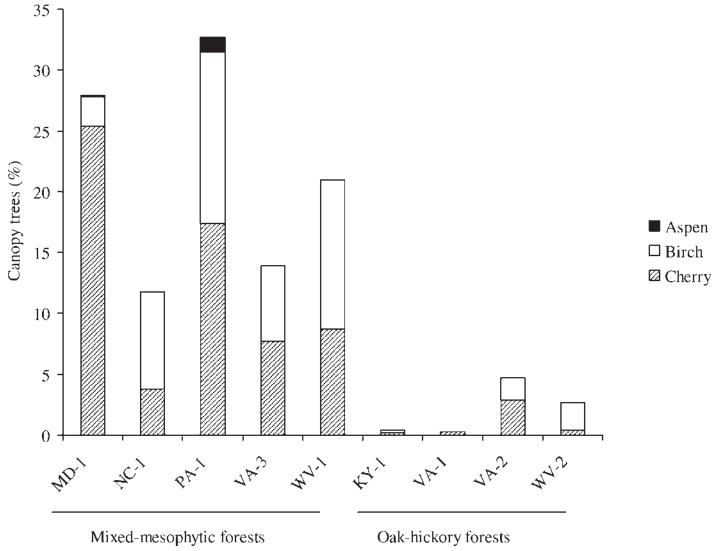

Figure 3. Percentage of canopy trees on study areas in the southern and central Appalachian region, USA, 1996–2002 represented by aspen, birch, and cherry. Data were collected at randomly located 0.04-ha plots (J. M. Tirpak, Fordham University, unpublished data; D. M. Whitaker, Virginia Polytechnic Institute and State University, unpublished data). Sample sizes varied across sites: MD-1 (*n* = 5,050), NC-1 (*n* = 5,587), PA-1 (*n* = 5,616), VA-3 (*n* = 7,259), WV-1 (*n* = 5,429), KY-1 (*n* = 3,825), VA-1 (*n* = 4,007), VA-2 (*n* = 6,142), and WV-2 (*n* = 7,804).

0.03 seen/hr) varied among sites. Predator species included raptors and mesomammals (Bumann 2002). Alternative prey species included rabbits (*Sylvilagus* spp.), squirrels (*Sciurus* spp.), and woodchucks (*Marmota monax*; Bumann 2002). Ruffed grouse hunting seasons typically opened in mid-October and ended the last week of February, but varied across states. Daily bag limits ranged from 2 birds to 4 birds per day. Exact season dates often varied from year to year.

METHODS

Field Methods

We trapped ruffed grouse from August to December (autumn) and February to April (spring) between 1996 and 2002 in lily-pad traps (Gullion 1965). We checked traps twice daily, once each in the morning and evening. We assumed that capturing and handling did not affect grouse behavior, habitat selection, or survival. Work in Ohio indicated radiotransmitters did not influence ruffed grouse survival (Swanson et al. 2003). We calculated trap rate as 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 calculated the flush rates as the number of grouse flushed from the vicinity of traps per 100 trap nights. We recorded the mass of each bird trapped and ascertained age and gender based on feather (i.e., primaries, tail, and rump) characteristics (Davis 1969, Kalla and Dimmick 1995). We classified each bird as juvenile (i.e., hatch-yr and entering first breeding season) or adult (i.e., after hatch-yr). Each bird was fitted with a uniquely numbered aluminum leg band and 10-g necklace-style radiotransmitter with an 8-hour mortality sensor (Advance Telemetry Systems, Isanti, MN) and released at the capture site. Released grouse had to survive a 7-day acclimation period before they were included in the study. After the 7-day acclimation period, ruffed grouse were monitored ≥ 2 times per week to ascertain their location (Whitaker 2003) and status (i.e., alive or dead).

We conducted qualitative evaluations of 6 mast-producing plant species (i.e., red or black oak, white oak, chestnut oak, beech, grape, and greenbrier) between August and December of each year on each study area. We ranked mast production of each species on a scale of 0–3 (i.e., 0 = complete mast failure, 1 = minimal mast crop, 2 = moderate mast crop, and 3 = abundant mast crop). If a species was not present on a particular study area, we recorded a score of zero. We calculated an annual mast production index for each study area [$Y = 7.96 + 6.72$(Chestnut Oak Score)] (Devers 2005). We derived this index through a model fitting exercise of female ruffed grouse preseason body condition (i.e., % body fat) and annual estimates of hard mast production (Devers 2005).

Reproductive Analysis

We monitored female ruffed grouse via radiotelemetry starting 1 April each year to determine reproductive activity. We considered birds triangulated in the same location over a period of 5 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 second or third week of incubation to ascertain clutch size and estimate hatch date. As the estimated hatch date approached, we monitored females daily via telemetry for signs of movement, which indicated hatching had occurred or the nest was lost (Vangilder and Kurzejeski 1995). Within 1 day of the female leaving the nest, we returned to the nest to document fate (i.e., successful or unsuccessful) and the number of eggs hatched. We considered nests successful if ≥ 1 egg hatched. We estimated the number of hatched eggs by counting eggshell fragments (Vangilder and Kurzejeski 1995). We monitored females with failed first nests ≥ 3 days per week to determine if

Table 2. Ruffed grouse reproductive parameters estimated in the southern and central Appalachian region, USA, 1997–2002.

Parameter	Description
Nesting rate	The proportion of F that attempted to nest as determined by radiotelemetry locations (Vangilder and Kurzejeski 1995).
Incubation date	Estimated by back dating from hatch date assuming a 24-d incubation period.
$\bar{x}$ clutch size	Determined by flushing nesting F during the second or third week of incubation and counting all visible eggs. Includes clutches of F killed during the incubation period.
Nest success	The proportion of nests from which $\geq$1 egg hatched. Includes nests of F killed during the incubation period (Roberts et al. 1995).
Renesting rate	The proportion of F with failed first nest attempts considered to have made a second nesting attempt (Vangilder and Kurzejeski 1995).
Hatching success	The proportion of eggs from successful first nests that ultimately hatched (Vangilder and Kurzejeski 1995).
F success	The proportion of F alive on 1 Apr that hatch $\geq$1 egg from a first or second nest.
35-d chick survival	The proportion of chicks in a brood alive at 35 d posthatch, including broods of F killed prior to 35 d posthatch.

a second nest was attempted. If a female attempted a second nest, we followed the same field protocols to ascertain nest fate, clutch size, nest success, and hatching success. We estimated chick survival to 35 days posthatch by following the radio signal of female to the brood, flushing the brood, and making ocular estimates of brood size on 35 day posthatch. All flush counts were conducted by $\geq$2 people. This method provided a minimum estimate of chick survival due to the possibility of under counting chicks. We calculated 35-day survival as:

$$S_{35\text{ - days}} = \frac{\text{No. chicks counted}}{\text{No. chicks hatched}}$$

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 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 developed post hoc models for clutch size (Burnham and Anderson 2002). We compared post hoc models of clutch size to the "best" a priori models. We conducted this post hoc analysis due to the poor fit of the original suite of a priori models and considered it an exploratory analysis. We obtained weather and temperature data from the National Climatic Data Center (NCDC 2004).

We used logistic regression (Proc Logistic; SAS Institute 2000) to fit a priori models of nest rate (NR), nest success (NS), renest rate (RNR), and female success (FS). We evaluated the fit for each global model (i.e., the most highly parameterized model) using a goodness-of-fit test (SAS Institute 2002). 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's Infor-

Table 3. Variables used to develop a priori models of factors affecting ruffed grouse reproductive ecology (RE), survival from 1997 to 2002 (S), and seasonal and annual survival (SAS) in the southern and central Appalachian region, USA, 1997–2002.

Variable	Model(s)	Description
Study area	RE, S, SAS	Dummy variable to indicate study area.
Yr	RE	Dummy variable to indicate yr of the investigation (i.e., 0–5).
Age	RE, S, SAS	Dummy variable to indicate the age of the F as either juv (first breeding season) or ad. Juv were graduated to ad each yr.
Mast	RE, S, SAS	An evaluation of the mast crop production in the autumn [$Y = 7.96 + 6.92$(Chestnut Oak Score); Devers 2005].
DP10	RE	The no. of d with $\geq$10 cm precipitation (National Oceanic and Atmospheric Administration [NCDC] 2004) in specified month or season.
DPNT	RE	Departure from normal monthly temp (NCDC 2004) in specified month or season.
MMNT	RE, SAS	Monthly $\bar{x}$ min. temp (NCDC 2004) in specified month or season.
TPCP	RE	Total precipitation (NCDC 2004) in specified month or season.
Month	RE	Temp and precipitation data used for specific months specified in the model.
Forest	RE, S, SAS	A classification of each site either oak–hickory or mixed-mesophytic forest association.
Time	S, SAS	Time indicates the time step used in survival analyses. The time step used for the 1997–2002 and annual analyses was a seasonal including spring (Apr–Jun), summer (Jul–Sep), autumn (Oct–Dec), and winter (Jan–Mar). The time step for the season-specific analysis was monthly.
Gender	S, SAS	Dummy variable to indicate the gender of the individual as M or F.
Mass	S	The mass of an individual at time of capture.
PREY	SAS	The $\bar{x}$ no. of rabbits (*Sylvilagus floridanus*) and squirrels (*Sciurus carolinensis*) observed/hr by month or season.
RAPTOR	SAS	The $\bar{x}$ no. of Cooper's hawks and owls (*Strix* spp.) observed/hr averaged by season. During the course of field activities biologists recorded all observations of Cooper's hawks and owls and calculated the no. seen divided by the no. of person hr. Observations were recorded on all study sites.
PPT	SAS	The total precipitation/month averaged by season.
SNOW	SAS	The $\bar{x}$ no. of d with crusted snow during winter.

mation Criterion (AIC_c), AIC_c differences (Δ_i), and Akaike weights (w_i; Burnham and Anderson 2002). We estimated relative likelihood of competing models by dividing the respective w_is (Burnham and Anderson 2002). We calculated AIC_c using the -2 log likelihood obtained using the "covout" option in Proc Logistic (SAS Institute 2002). We used the quasi-likelihood adjustment ($QAIC_c$) if we detected overdispersion in the data. We tested for overdispersion ($\hat{C}$) in the global model based on a single variance inflation factor ($\alpha = 0.15$) approximated with the formula (Burnham and Anderson 2002):

$$\hat{C} = \chi^2/\mathrm{df}.$$

We also report percent concordant, percent discordant, and percent tied observations to facilitate model evaluation.

We used general linear mixed models (JMP 1996) to evaluate the ability of our a priori models to explain variation in incubation date (INCD), clutch size (Clutch), and hatching success (Hatch). We evaluated the fit of each global model by evaluating the global analysis of variance (ANOVA) test and visually inspecting residuals. We used AIC_c, Δ_i, and w_i (Burnham and Anderson 2002) to rank and evaluate models. We estimated relative likelihood of competing models by dividing their respective w_is (Burnham and Anderson 2002). We report R^2 and R^2_{adj} to aid model evaluation (Eberhardt 2003). We considered models with Δ_i of approximately 2.0 as competing models (Burnham and Anderson 2002). We tested for pair-wise correlation among continuous explanatory variables and removed one 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 (D. R. Anderson, United States Geological Survey Cooperative Extension Unit, Colorado State University, personal communication). We report effect sizes for parameters that do not contain zero in the 95% confidence interval.

Survival Analysis

We obtained survival and cause-specific mortality data by tracking radiomarked grouse ≥ 2 times per week and recording status as alive or dead. After detecting a mortality signal, we located the carcass and ascertained the cause of death based on carcass remains, predator sign in the immediate vicinity, and markings on the radiotransmitter (Bumann 2002). Cause of death was recorded as avian predation, mammalian predation, unknown predation, or natural. The date of mortality was assigned as the midpoint between the last known alive date and the date mortality was discovered (Pollock et al. 1989*a*, *b*). Birds that could not be located due to emigration from the study area or failed radiotransmitter were right-censored (Pollock et al. 1989*a*, *b*). We assigned the date of censoring as the day after the last known date alive. We collected data about the location and date of harvested birds using a $25 reward inscribed on the radiotransmitter and leg band. We assigned cause of death as crippling loss if a recovered bird showed signs of harvest (e.g., presence of pellets in the body). We assigned the cause of death as illegal harvest based on information gained through law enforcement activities.

Kaplan–Meier.—We estimated site-specific annual survival rates (pooled across age and gender class) using the staggered entry design (Pollock et al. 1989*a*, *b*) 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 more than once each week in all seasons. Seasons were spring (1 Apr–30 Jun), summer (1 Jul–30 Sep), autumn (1 Oct–31 Dec), and winter (1 Jan–31 Mar). We estimated annual survival rates using the known fates model in Program MARK (White and Burnham 1999) to provide estimates comparable to previous studies using similar methods. We calculated the percentage of mortality due to a specific cause by dividing the number of mortalities due to each cause by the total number of mortalities during the period of interest. We calculated cause-specific mortality rates by censoring all deaths except the cause of interest (e.g., avian predation; Trent and Rongstad 1974).

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. We conducted all analyses using Program MARK (White and Burnham 1999). We selected explanatory variables and developed a priori models based on published literature (Bump et al. 1947, Rusch and Keith 1971, Small et al. 1991) and our experience. We ascertained the appropriate time step by fitting the global (or Full) model using a 15-day, monthly, and seasonal (spring, summer, autumn, winter) time step and comparing estimates of $\hat{C}$. We then used the time step (i.e., season) 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 Apr 1997–31 Mar 2002). In the trade-off between duration and missing observations, this data set consisted of the fewest explanatory variables (Table 3) and a priori models. Second, we analyzed survival in 5 1-year periods (1 Apr–31 Mar). These data sets included different combinations of study areas depending on data completeness. They also included additional explanatory variables including raptor abundance, alternative prey abundance, snow conditions (Bumann 2002), and temperature (Table 3) 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 w_i to rank and evaluate models (Burnham and Anderson 2002). We estimated relative likelihood of competing models by dividing the respective to w_i's (Burnham and Anderson 2002). We used $\hat{C}$ from the global model to correct for overdispersion 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 (D. R. Anderson, personal communication). We drew conditional inference based on single models. We report effect

Table 4. Parameters used in the development of deterministic (models 1 and 2) ruffed grouse population models. Mean reports the mean parameter value used in model development.

Parameter	Models	$\bar{x}$	Description
Nest rate	1	0.94	Proportion of F alive on 1 Apr that attempt to nest.
Nest success	1	0.66	Proportion of F that attempt to nest that hatch $\geq$1 chick.
Clutch	1	9.67	No. eggs laid.
Hatching success	1	0.96	Proportion of eggs in a clutch that hatch.
Renest rate	1	0.24	Proportion of F with failed first nest attempts that attempt to lay a second clutch.
Second nest success	1	0.55	Proportion of F that attempt a second nest that hatch $\geq$1 chick.
Second clutch size	1	7.0	No. eggs laid in a second nest attempt.
Second hatching success	1	0.49	Proportion of eggs in a second clutch that hatch.
Chick survival	1	0.22	Probability of a chick surviving to 35 d posthatch as a function of mast production the previous autumn ($B = 0.132 + 0.007 \times M$).
Chick production	2	0.92	No. chicks age 35 d posthatch/F alive on 1 Apr as a function of mast production the previous autumn ($F' = 1.16 + 0.052 \times M$).
Spring survival	1, 2	0.80	Probability of an ad grouse surviving the spring season.
Summer survival	1, 2	0.92	Probability of an ad grouse surviving the summer season.
Autumn survival	1, 2	0.79	Probability of an ad grouse surviving the autumn season.
Winter survival	1, 2	0.74	Probability of an ad grouse surviving the winter season.
Mast index	1, 2	13.15	Index of hard mast production in the autumn [$Y = 7.96 + 6.92$(Chestnut Oak Score); Devers 2005].

sizes for variables with point estimates and 95% confidence intervals. We report models with Δ_is $\leq$10.0 and w_is $\geq$0.05 for all model selection analyses (i.e., reproductive and survival analyses). A complete list of a priori models and model selection results are provided in Devers (2005).

Test of the Compensatory Mortality Hypothesis

We tested the compensatory mortality hypothesis by conducting a manipulative field experiment on 7 study areas (Table 1). We used data from only those study areas that were active during both phases of the study. Phase I of the study was autumn 1996–summer 1999 and Phase II was autumn 1999–summer 2002. We based the experimental design on a completely randomized design with repeated measures. Four study areas (i.e., MD-1, VA-1, VA-2, and WV-1) were assigned as the control group (i.e., open) and 3 sites (i.e., KY-1, VA-3, and WV-2) were assigned as the treatment group (i.e., closed). Control sites were open to ruffed grouse hunting during each phase of the study. We closed treatment sites to ruffed grouse hunting during Phase II. We used a repeated measures ANOVA to test for the main effects of treatment (i.e., open or closed to hunting) and phase on annual survival and reproductive effort (i.e., nesting rate, nest success, female success, and chick survival). We also tested for interactions between treatment and phase. A significant 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 apply treatments randomly to study areas. Instead, we closed the 3 study areas with the highest harvest rates during 1996–1998 seeking to impose the largest effect possible on the experiment. We estimated annual survival (1 Apr–31 Mar) using the staggered entry design (Pollock 1989 *a*, *b*) modification of the product limit estimator (Kaplan and Meier 1958) as described above. Due to limited sample size, we estimated annual survival by treatment, age, gender, and pooled across age and gender classes. We estimated cause-specific mortality rates using the Kaplan–Meier method after censoring all mortalities due to causes except the one of interest (i.e., harvest; Trent and Rongstad 1974). We calculated percentage of mortality due to a specific cause 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 ruffed grouse population models to estimate finite population growth rate (λ) and assess the influence of vital rates on λ. 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 variable tracked over time was population size and the final output was $\overline{\lambda}$ 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 (Edminster and Crissey 1947), resulting in 4 age classes. Based on our reproductive and survival analyses, we assumed vital rates did not differ among age classes.

We developed each model at 3 spatial bounds, including central and southern Appalachian region, forest association, and study area using data collected as part of the ACGRP. The regional model was developed using parameter values pooled across study areas (except OH-1 and OH-2 because they were not classified as either oak–hickory or mixed-mesophytic forests) and averaged across years (Table 4). The objective of this scale was to understand regional ruffed grouse population dynamics in the Appalachians. To validate the deterministic models, we compared our estimated 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 and oak–hickory forests to regional population dynamics. We developed the mixed-mesophytic forest model

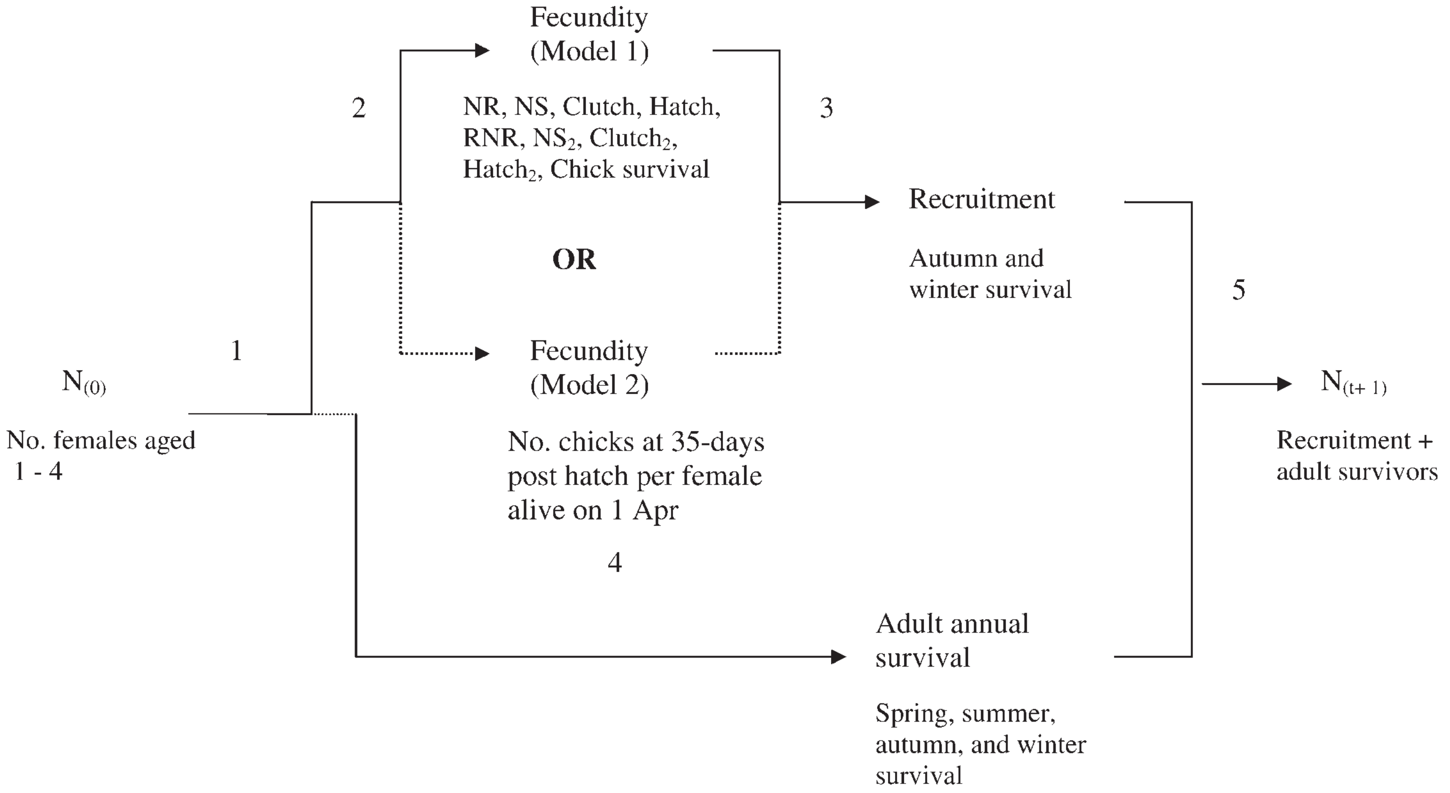

Figure 4. Schematic of modeling process for deterministic models 1 and 2. Models differ in the estimate of fecundity (i.e., step 2). Model variables include population size at time t (N_t), mean nest rate (NR), mean nest success (NS), mean clutch size (Clutch), mean hatching success (Hatch), mean renest rate (RNR), mean nest success of second attempt (NS_2), mean clutch size of second attempt ($Clutch_2$), mean hatching success of second attempt ($Hatch_2$), chick survival to 35 days posthatch, juvenile recruitment to the spring population (Recruitment), and adult annual survival.

using parameter estimates pooled across study areas classified as mixed-mesophytic forests and averaged across years. We estimated parameters for the oak–hickory forest model by pooling data across study areas identified as dominated by oak–hickory forest association and averaged across years. We developed the mixed-mesophytic study area model using parameter estimates averaged across study areas classified as mixed-mesophytic and years. We developed the oak–hickory study area model 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 wildlife management areas. We were unable to validate our estimates of λ at the forest or study area scale due to a lack of similar spatial scale estimates in the Breeding Bird Survey.

We 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. Each time step started on 1 April with reproduction by adults (ages 1–4), followed by recruitment, and finally survival of adults, resulting in estimated abundance of birds ages 1–4. Juvenile birds became adults on 1 April of the year after hatch. We conducted elasticity analyses to assess the influence of vital rates on λ.

Model 1.—The first model (Fig. 4) estimated mean fecundity (F), defined as the number of female offspring produced in unit of time (Krebs 1994), and used it at each time step. We estimated F as function of multiple secondary vital rates (Table 4) using the formula:

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

Where $N =$ number of females (ages 1–4) on 1 April, $E =$ mean nesting rate, $G =$ mean nest success rate, $C =$ mean clutch size, $H =$ mean hatching success, $I =$ mean renest rate, $J =$ mean nest success rate for second nests, $K =$ mean clutch size for second nests, $L =$ mean hatching success for second nests, $B =$ mean 35-day chick survival rate as a function of mean mast production (M; Table 4), and $X =$ 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 the incremental increase to a natural population, usually from juvenile animals entering the breeding population (Krebs 1994), and was calculated using the formula:

$$R = F \times S_a \times S_w$$

where $F =$ fecundity, $S_a =$ autumn survival rate, and $S_w =$ winter survival rate. We calculated the female population size using equations

$$N_{t+1} = N_t \times S' + R$$

where $N =$ number of female ruffed grouse (ages 1–4), $t =$ year, and $S' =$ annual adult survival rate

Table 5. Ruffed grouse autumn trap success in the southern and central Appalachian region, USA, by study area, 1996–2002. Sample size (n) refers to the number years.

	Grouse/100 trap nights				Flushes/100 trap nights[a]			
Study area	n	$\bar{x}$	SE	95% CI	n	$\bar{x}$	SE	95% CI
KY-1	6	1.41	0.314	0.60–2.21	6	0.60	0.215	0.05–1.15
MD-1	6	2.17	0.482	0.83–3.51	6	1.81	0.454	0.55–3.07
NC-1	3	0.89	0.135	0.31–1.47	—	—	—	—
OH-1	1	3.2	—	—	1	1.03	—	—
OH-2	2	4.59	0.930	0.0–16.41	2	1.66	1.050	0.0–15.00
PA-1	4	6.00	1.23	2.06–9.92	4	1.98	0.201	1.34–2.62
RI-1	3	1.23	0.289	0.0–2.48	3	0.51	0.182	0.0–1.29
VA-1	5	0.87	0.168	0.41–1.34	5	2.22	0.384	1.16–3.29
VA-2	6	1.06	0.322	0.23–1.88	6	1.27	0.236	0.66–1.88
VA-3	6	1.13	0.065	0.96–1.29	6	0.35	0.087	0.13–0.58
WV-1	6	3.00	0.391	2.00–4.00	6	2.13	0.481	0.90–3.37
WV-2	6	4.71	0.551	3.29–6.13	—	—	—	—

[a] Defined as the no. of birds flushed from the vicinity of a trap during routine trapping activities.

$$S' = S_{\mathrm{p}} \times S_{\mathrm{s}} \times S_{\mathrm{a}} \times S_{\mathrm{w}}$$

where S_{p} = spring survival rate, S_{s} = summer survival rate, S_{a} = autumn survival rate, and S_{w} = winter survival rate. Finite growth rate (λ) was calculated using the formula

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

Model 2.—Deterministic model 2 (Fig. 4) was structurally the same as model 1. We estimated recruitment and survival in the same manner, but fecundity was estimated using 1 parameter. We defined fecundity (F') as the number of chicks alive at 35 days posthatch per adult female alive on 1 April. By consolidating fecundity into 1 parameter, we were able to incorporate correlation among secondary vital rates (e.g., nest rate and nest success) and potentially decrease measurement error. In models 1 and 2 we modeled fecundity as a function of mean mast production (Table 4).

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. We calculated the proportion of the population in each age class at each time step until a stable age distribution was obtained. We used the estimated stable age distribution for all subsequent model runs.

Table 6. Autumn age ratios (juv, F, and ad) of trapped ruffed grouse in the southern and central Appalachian region, USA, by study area, 1996–2001. Sample size (n) refers to the number of years.

	Juv:ad F				Juv F:ad			
Study area	n	$\bar{x}$	SE	95% CI	n	$\bar{x}$	SE	95% CI
KY-1	6	0.53	0.127	0.21–0.86	6	0.30	0.084	0.09–0.52
MD-1	6	1.31	0.592	0.0–2.83	6	0.70	0.345	0.0–1.59
NC-1	3	0.53	0.174	0.0–1.28	3	0.32	0.115	0.0–0.81
OH-1	3	0.45	0.164	0.0–1.15	3	0.27	0.120	0.0–0.79
OH-2	4	0.36	0.110	0.02–0.71	4	0.19	0.058	0.00–0.37
PA-1	4	0.74	0.137	0.31–1.18	4	0.38	0.069	0.16–0.60
RI-1	3	0.47	0.168	0.0–1.19	3	0.18	0.111	0.0–0.66
VA-1	5	1.03	0.336	0.10–1.97	5	0.44	0.197	0.0–0.99
VA-2	6	0.24	0.074	0.05–0.43	6	0.13	0.044	0.02–0.24
VA-3	6	0.28	0.064	0.11–0.44	6	0.17	0.030	0.09–0.24
WV-1	6	0.32	0.074	0.12–0.51	6	0.12	0.039	0.02–0.22
WV-2	6	0.42	0.104	0.15–0.68	6	0.15	0.052	0.02–0.29

Table 7. Ruffed grouse reproductive rates in the southern and central Appalachian region, USA, 1997–2002 (pooled across sites and yr).

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 Apr–2 May
Clutch size	368	9.86	0.111	9.64–10.07
Hatching success[a]	384	0.82	—	—
Nest success	410	0.66	0.023	0.62–0.71
Renest rate	111	0.23	0.040	0.16–0.31
F success	411	0.68	0.023	0.64–0.73
35-d chick survival	235	0.22	0.016	0.19–0.25

[a] We report median hatching success due to skewness of the data.

Elasticity analyses.—We preformed 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 one demographic parameter (holding all others constant) from 10% to 90% of the mean value in increments of 10 and calculated λ. We repeated this process for each demographic parameter in the model and identified which parameters had the greatest influence on λ.

RESULTS

We captured 3,118 ruffed grouse between autumn 1996 and spring 2002, including 413 recaptures. The mean trap rate (averaged across sites and yr) was 2.37 grouse per 100 trap nights ± 0.26 (SE; 95% CI = 1.84–2.90 grouse/100 trap nights; Table 5). Mean trap flush rate (during the course of checking traps; averaged across sites and yr) was 1.37 ± 0.15 flushes per 100 trap nights (95% CI = 1.07–1.67 flushes/100 trap nights, Table 5). The mean juvenile:adult female ratio was 0.56 ± 0.08 (95% CI = 0.40–0.72, Table 6) and the mean juvenile female:adult female ratio was 0.28 ± 0.05 (95% CI = 0.19–0.37, Table 6).

Reproductive Analysis

We monitored 467 females during nest and brood seasons during 1997–2002 and estimated mean nest rate, nest initiation date, clutch size, renest rate, nest success, female success, and chick survival (Table 7).

Nesting rate.—The overall NR was 0.96 (Table 7). The final data set used to model NR consisted of 279 records from spring 1997 to spring 2002. This final data set did not include records from OH-1, OH-2, or NC-1 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 19, Table 8) indicated NR 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 NR was higher in mixed-mesophytic forests ($\bar{x} = 1.0$, ± 0.0, $n = 147$) than in oak–hickory forests ($\bar{x} = 0.86$, ± 0.030, 95% CI = 0.80–0.92, $n = 132$); NR ranged from

Table 8. A priori models and results of information theoretic model selection process of ruffed grouse nesting rate (NR) in the southern and central Appalachian region, USA, 1997–2002 ($n = 279$).[a]

Model	Description	K[b]	Log L[c]	AIC$_c$	Δ_i	w_i	% concordant[d]	% discordant[e]	% tied[f]
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

[a] Models were fit using logistic regression. Model variables include intercept (β_0), forest association (i.e., classification of each study site as oak–hickory or mixed-mesophytic forest association based on canopy tree species composition; Forest), yr (YR), and variance (ε). AIC$_c$ is Akaike's Information Criterion adjusted for small sample size, Δ_i is AIC$_c$ differences, and w_i is Akaike wt.

[b] No. of estimated parameters in the model.

[c] Log likelihood estimate.

[d] % observation correctly predicted by the logistic regression model.

[e] % observation incorrectly assigned to a group by the logistic regression model.

[f] % observations that could not be assigned to either group.

Table 9. A priori models and results of information theoretic model selection process of ruffed grouse incubation date (INCD) in the southern and central Appalachian region, USA, 1997–2002 ($n = 176$).[a]

Model	Description	K[b]	RSS[c]	Log L[d]	AIC$_c$	Δ_i	w_i	R^2	R^2_{adj}
10	INCD = β_0 + Age + SA + YR + Mast + DPNT$_{(\mathrm{win})}$ + MMNT$_{(\mathrm{win})}$ + (Mast × MMNT$_{(\mathrm{win})}$) + ε	16	6,257.30	−314.25	663.92	0.00	0.69	0.40	0.35
35	INCD = β_0 + Forest + SA(Forest) + YR + Forest × YR + ε	15	6,464.80	−317.12	667.24	3.32	0.13	0.38	0.33
17	INCD = β_0 + SA + Age + YR + DPNT$_{(\mathrm{win})}$ + ε	10	6,959.61	−323.61	668.55	4.63	0.07	0.33	0.30
19	INCD = β_0 + SA + Age + Mast + DPNT$_{(\mathrm{win})}$ + (Mast × DPNT$_{(\mathrm{win})}$) + ε	12	6,791.28	−321.46	666.91	4.91	0.06	0.35	0.31

[a] Models were fit using linear regression. Model variables include intercept (β_0), age of individual birds (i.e., juv or ad; Age), study area (SA), yr (YR), index of annual hard mast production (Mast), departure from normal monthly temp in winter (DPNT$_{(\mathrm{win})}$), monthly $\bar{x}$ min. temp in winter (MMNT$_{(\mathrm{win})}$), forest association (i.e., classification of each study site as oak–hickory or mixed-mesophytic forest association based on canopy tree species composition; Forest), and variance (ε). AIC$_c$ is Akaike's Information Criterion adjusted for small sample size, Δ_i is AIC$_c$ differences, and w_i is Akaike wt.

[b] No. of estimated parameters in the model.

[c] Residual sum of squares.

[d] Log likelihood estimate.

0.71 to 1.0 across years in oak–hickory forests. The remaining models did not receive support as competing models (Table 8).

Incubation date.—Mean date of incubation initiation for 351 nests was 1 May (Table 7). 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 9). Mean INCD ranged from 27 April to 8 May across study areas. Adult females initiated incubation 3.5 ± 0.88 days (95% CI = 1.8–5.3 d) earlier than juvenile females. Remaining parameters (Mast, departure from normal monthly temp in winter [DPNT$_{(\mathrm{win})}$], and monthly $\bar{x}$ min. temp in winter [MMNT$_{(\mathrm{win})}$]) had confidence intervals for the β_is that included zero.

Clutch size.—Mean clutch size was 9.86 eggs (Table 7). The clutch size data set included 211 observations (Table 10). 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 10), thus we

Table 10. A priori models and results of information theoretic model selection process of ruffed grouse clutch size (Clutch) in the southern and central Appalachian region, USA, 1997–2002 ($n = 211$).[a]

Model	Description	K[b]	RSS[c]	Log L[d]	AIC$_c$	Δ_i	w_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

[a] Models were fit using linear regression. Model variables include intercept (β_0), study area (SA), age of individual birds (i.e., juv or ad; Age), yr (YR), index of annual hard mast production (Mast), forest association (i.e., classification of each study site as oak–hickory or mixed-mesophytic forest association based on canopy tree species composition; Forest), and variance (ε). AIC$_c$ is Akaike's Information Criterion adjusted for small sample size, Δ_i is AIC$_c$ differences, and w_i is Akaike wt.

[b] No. of estimated parameters in the model.

[c] Residual sum of squares.

[d] Log likelihood estimate.

Table 11. Post hoc information theoretic model selection process of ruffed grouse clutch size (Clutch) in the southern and central Appalachian region, USA, 1997–2002 ($n = 186$).[a]

Model	Description	K[b]	RSS[c]	Log L[d]	AIC$_c$	Δ_i	w_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[e]	Clutch = β_0 + Forest + Mast + SA(Forest) + ε	8	610.64	−110.56	237.92	9.68	0.01	0.10	0.07
1[e]	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] Model variables include intercept (β_0), study area (SA), age of individual birds (i.e., juv or ad; Age), index of annual hard mast production (Mast), forest association (i.e., classification of each study site as oak–hickory or mixed-mesophytic forest association based on canopy tree species composition; Forest), incubation date (INCD), nest fate (binomial classification of the fate of the first nest attempt as either disturbed or not disturbed; disturbed nests were either abandoned or partially predated; NF), and variance (ε). AIC$_c$ is Akaike's Information Criterion adjusted for small sample size, Δ_i is AIC$_c$ differences, and w_i is Akaike wt.

[b] No. of estimated parameters in the model.

[c] Residual sum of squares.

[d] Log likelihood estimate.

[e] These were most supported a priori models (Table 10).

developed several post hoc models to gain more insight into variation in clutch size (Table 11). 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 11). Model E received the greatest support (Table 11) 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 within forest associations, and incubation date. Mean clutch size was larger in mixed-mesophytic forests than in oak–hickory forests by 0.97 ± 0.238 eggs (95% CI = 0.49–1.45 eggs). Mean clutch size ranged from 9.6 to 11.2 eggs across study areas and was negatively related to nest initiation date ($\beta = -0.071 \pm 0.022$, 95% CI = −0.114 to −0.029).

Hatching success.—The complete data set for hatching success (HS) included 384 nests. Median HS of 384 nests was 0.82 (Table 7). The HS data set used in the model selection procedure contained 144 observations. However, model selection was not conducted due to the poor fit of the global model ($F_{17,126} = 0.8126$, $P = 0.676$).

Nest success.—The overall NS was 0.66 for 410 nests (Table 7). 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 NS, but no single model was clearly better than the others (Table 12). The most supported model (model 16) indicated variation in NS was a function of mast production ($\beta_{\text{logit}} = -0.507 \pm 0.231$, 95% CI = −0.959 to −0.055), MMNT$_{(\text{Mar \& Apr})}$ ($\beta_{\text{logit}} = -0.196 \pm 0.0898$, 95% CI = −0.372 to −0.02), and an interaction between mast × MMNT$_{(\text{Mar \& Apr})}$ ($\beta_{\text{logit}} = 0.016 \pm 0.007$, 95% CI = 0.002–0.029). Models 1 and 8 received limited support (Table 12) and indicated mean NS varied across study areas (0.53–0.94) and years. Mean NS did not differ between mixed-mesophytic forests ($\bar{x} = 0.70 \pm 0.040$, 95% CI = 0.62–0.78, $n = 131$) and oak–hickory forests ($\bar{x} = 0.63 \pm 0.050$ SE, 95% CI = 0.53–0.73, $n = 95$).

Table 12. A priori models and results of information theoretic model selection process for ruffed grouse nest success (NS) in the southern and central Appalachian region, USA, 1997–2002 ($n = 226$).[a]

Model	Description	K[b]	Log L[c]	AIC$_c$	Δ_i	w_i	% concordant[d]	% discordant[e]	% tied[f]
16	NS = β_0 + Mast + MMNT$_{(\text{Mar \& Apr})}$ + (Mast × MMNT$_{(\text{Mar \& Apr})}$) + 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

[a] Models were fit with logistic regression. Model variables include intercept (β_0), study area (SA), yr (YR), index of annual hard mast production (Mast), forest association (i.e., classification of each study site as oak–hickory or mixed-mesophytic forest association based on canopy tree species composition; Forest), monthly $\bar{x}$ min. temp in Mar and Apr (MMNT$_{(\text{Mar \& Apr})}$), and variance (ε). AIC$_c$ is Akaike's Information Criterion adjusted for small sample size, Δ_i is AIC$_c$ differences, and w_i is Akaike wt.

[b] No. of estimated parameters in the model.

[c] Log likelihood estimate.

[d] % observation correctly predicted by the logistic regression model.

[e] % observation incorrectly assigned to a group by the logistic regression model.

[f] % observations that could not be assigned to either group.

Table 13. A priori models and results of information theoretic model selection process for ruffed grouse renest rate (RNR) in the southern and central Appalachian region, USA, 1997–2002 ($n = 64$).[a]

Model	Description	K[b]	Log L[c]	QAIC$_c$	Δ_i	w_i	% concordant[d]	% discordant[e]	% tied[f]
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$_{(\text{win})}$	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$_{(\text{win})}$	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

[a] Models were fit with logistic regression. Model variables include intercept (β_0), age of individual birds (i.e., juv or ad; Age), index of annual hard mast production (Mast), forest association (i.e., classification of each study site as oak–hickory or mixed-mesophytic forest association based on canopy tree species composition; Forest), and variance (ε). QAIC$_c$ is Akaike's Information Criterion adjusted for small sample size and quasi-likelihood, Δ_i is AIC$_c$ differences, and w_i is Akaike wt.

[b] No. of estimated parameters in the model.

[c] Log likelihood estimate.

[d] % observation correctly predicted by the logistic regression model.

[e] % observation incorrectly assigned to a group by the logistic regression model.

[f] % observations that could not be assigned to either group.

Renest rate.—Overall RNR was 0.23 (Table 7). Our RNR data set consisted of 64 records from MD-1, PA-1, VA-1, VA-2, WV-1, and WV-2. 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 overdispersion ($\hat{C} = 1.27$) in the data. Three models were considered to be competing (Table 13). 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 RNR was a function of differences in forest associations. Mean RNR was higher in mixed-mesophytic forests ($\bar{x} = 0.45 \pm 0.088$, 95% CI = 0.28–0.62) than in oak–hickory forests ($\bar{x} = 0.03 \pm 0.032$, 95% CI = 0.00–0.10). Model 6 indicated RNR was negatively correlated with MMNT$_{(\text{win})}$ ($\beta_{\text{logit}} = -0.188 \pm 0.095$ SE., 95% CI = −0.375 to −0.002). Similar to model 23, model 9 suggested RNR was a function of differences in forest associations and mast production the previous autumn. Estimated beta value and confidence interval for mast included zero.

Female success.—Overall mean FS for 412 females was 0.68 (Table 7). The FS 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 FS (Table 14). The 3 competing models indicated variation in FS 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 FS did not differ between mixed-mesophytic ($\bar{x} = 0.70$, 95% CI = 0.4–0.92, $n = 133$) and oak–hickory forests ($\bar{x} = 0.63$, 95% CI = 0.56–0.83, $n = 99$). Beta estimates and confidence intervals for mast and interaction terms overlapped zero.

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 7). 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 15). Model 4 was the best model and was 3.44 times more likely than the next most supported model but the explanatory power was extremely low ($R^2 = 0.04$; Table 15). Model 4 indicated chick survival to 35 days posthatch was positively related to mast production ($\beta = 0.003 \pm 0.001$, 95% CI = 0.00–0.005). Mean 35-day chick survival (pooled across study areas and yr) was 0.21 ± 0.019, (95% CI = 0.18–0.25, $n = 145$).

Survival Analysis

Kaplan–Meier.—Mean annual survival of ruffed grouse (averaged across sites and yr) in the Appalachian region was

Table 14. A priori models and results of information theoretic model selection process of ruffed grouse female success (FS) in the southern and central Appalachian region, USA, 1997–2002 ($n = 230$).[a]

Model	Description	K[b]	Log L[c]	QAIC$_c$	Δ_i	w_i	% concordant[d]	% discordant[e]	% tied[f]
28	FS = β_0 + Forest + Mast + Forest × Mast + ε	3	−136.56	279.22	0.00	0.24	57.2	33.9	8.9
26	FS = β_0 + Forest + Mast + ε	3	−136.59	279.29	0.07	0.23	56.7	34	9.4
24	FS = β_0 + Forest + ε	2	−138.06	280.17	0.95	0.15	34.8	16.6	48.6
19	FS = β_0 + Forest + Age + Mast + ε	4	−136.56	281.30	2.08	0.08	59.5	35.8	4.7
15	FS = β_0 + Mast + MMNT$_{(\text{Mar \& Apr})}$ + (Mast × MMNT$_{(\text{Mar \& Apr})}$) + ε	4	−137.15	282.48	3.25	0.05	59	35.7	5.3

[a] Models were fit with logistic regression. Model variables include intercept (β_0), age of individual birds (i.e., juv or ad; Age), index of annual hard mast production (Mast), forest association (i.e., classification of each study site as oak–hickory or mixed-mesophytic forest association based on canopy tree species composition; Forest), monthly $\bar{x}$ min. temp in Mar and Apr (MMNT$_{(\text{Mar \& Apr})}$), and variance (ε). QAIC$_c$ is Akaike's Information Criterion adjusted for small sample size and quasi-likelihood, Δ_i is AIC$_c$ differences, and w_i is Akaike wt.

[b] No. of estimated parameters in the model.

[c] Log likelihood estimate.

[d] % observation correctly predicted by the logistic regression model.

[e] % observation incorrectly assigned to a group by the logistic regression model.

[f] % observations that could not be assigned to either group.

Table 15. A priori models and results of information theoretic model selection process for ruffed grouse chick survival to 35 days posthatch (S_{35}) in the southern and central Appalachian region, USA, 1997–2002 ($n = 145$).[a]

Model	Description	K[b]	RSS[c]	Log L[d]	AIC$_c$	Δ_i	w_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	$S_{35} = \beta_0 + \text{Mast} + \text{Forest} + \text{Mast} \times \text{Forest}$	5	7.503	181.55	−352.67	3.32	0.06	0.05	0.03
17	$S_{35} = \beta_0 + \text{INCD} + \text{Forest} + \text{INCD} \times \text{Forest}$	5	7.510	181.49	−352.55	3.44	0.06	0.04	0.02

[a] Models were fit using linear regression. Model variables include intercept (β_0), index of annual hard mast production (Mast), forest association (i.e., classification of each study site as oak–hickory or mixed-mesophytic forest association based on canopy tree species composition; Forest), incubation date (INCD), the no. of d with >10 cm precipitation (DP10), and variance (ε). AIC$_c$ is Akaike's Information Criterion adjusted for small sample size, Δ_i is AIC$_c$ differences, and w_i is Akaike wt.

[b] No. of estimated parameters in the model.

[c] Residual sum of squares.

[d] Log likelihood estimate.

0.42 ± 0.022 (95% CI = 0.38–0.46) and ranged from 0.17 to 0.57 across study areas (Table 16). Avian predation was the leading cause of known mortalities, followed by mammalian predation (Fig. 5). Harvest (including legal and illegal harvest and crippling loss) accounted for 11.7% of all known mortalities. Estimates of cause-specific mortality rates produced similar results. Avian predation rate was higher ($\bar{x} = 0.32 \pm 0.020$, 95% CI = 0.28–0.36) than other cause-specific mortality rates including mammalian predation rate ($\bar{x} = 0.21 \pm 0.018$, 95% CI = 0.17–0.24), and predation rate by unidentified predators ($\bar{x} = 0.13 \pm 0.025$, 95% CI = 0.08–0.18). Mean natural mortality rate was 0.54 (±0.023, 95% CI = 0.50–0.59). Mean harvest rate across sites and years was 0.10 (±0.014, 95% CI = 0.07–0.13) excluding treatment sites between 1999 and 2002.

Survival 1997–2002.—We modeled ruffed grouse survival from April 1997 to March 2002 using data from MD-1, VA-2, VA-3, WV-1, and WV-2 with records for 1,064 individual ruffed grouse. There was evidence of overdispersion in the data ($\hat{C} = 3.14$), but residuals were normally distributed. The best model (model 5, Table 17) indicated survival was a function of differences between oak–hickory and mixed-mesophytic forest associations and seasonal variation. Survival was higher ($\bar{x}$ difference = 0.03, 95% CI = 0.01–0.06) on oak–hickory forests than on mixed-mesophytic forests and was highest in summer and lowest in winter (Fig. 6). This model was 1.6 times more likely to be the best model than the next competing model (Table 17).

Model 14 received moderate support ($w_{14} = 0.30$) and indicated ruffed grouse survival during this period was a function of differences in forest associations, age, and season. Survival was higher in oak–hickory forests than in mixed-mesophytic forests ($\bar{x}$ difference = 0.02, 95% CI = 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 zero.

Survival 1997–1998.—Our data set for April 1997 to March 1998 survival analysis consisted of 273 individual grouse from MD-1, VA-2, VA-3, WV-1, and WV-2. The global model provided adequate fit ($\hat{C} = 2.45$) and the residuals were normally distributed. The best model (model 2, Table 18) indicated survival varied by season. Survival was highest in summer ($\bar{x} = 0.94$, 95% CI = 0.89–0.97), followed by spring ($\bar{x} = 0.82$, 95% CI = 0.75–0.88), autumn ($\bar{x} = 0.79$, 95% CI = 0.72–0.83), and winter ($\bar{x} = 0.72$, 95% CI = 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.

Table 16. Mean annual survival rates (pooled across gender and age classes) of ruffed grouse in the southern and central Appalachian region by study area and averaged across years.[a]

Study area	n	$\bar{x}$	SE	95% CI
KY-1	5	0.40	0.03	0.34–0.46
MD-1	5	0.35	0.017	0.32–0.38
NC-1	2	0.33	0.045	0.24–0.42
OH-1	2	0.55	0.025	0.50–0.62
OH-2	2	0.17	0.085	0.00–0.34
PA-1	3	0.29	0.044	0.20–0.38
RI-1	2	0.30	0.09	0.12–0.48
VA-1	4	0.56	0.037	0.49–0.63
VA-2	5	0.49	0.063	0.37–0.61
VA-3	5	0.33	0.05	0.23–0.43
WV-1	5	0.47	0.047	0.38–0.56
WV-2	5	0.57	0.071	0.43–0.72

[a] Estimates were obtained using the Kaplan–Meier product limit estimator in Program MARK. Sample size (n) refers to the no. of yr.

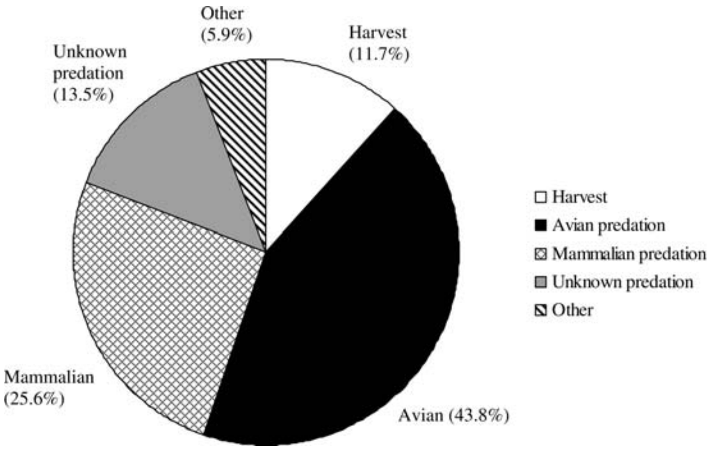

Figure 5. Percentage of known ruffed grouse mortalities averaged across study areas and years ($n = 45$) by cause in the southern and central Appalachian region, USA, 1997–2002.

Table 17. A priori models and model selection results of ruffed grouse survival (S) in the southern and central Appalachian region, USA, April 1997–March 2002.[a]

Model	Description	K[b]	QAIC$_c$[c]	Δ_i[d]	w_i[e]
5	$S = \beta_0$ + Forest + Season (cloglog) + ε	22	1,937.87	0.00	0.48
14	$S = \beta_0$ + Forest + Age + Season (cloglog) + ε	23	1,938.77	0.90	0.30
15	$S = \beta_0$ + Forest + Gender + Season + (logit) + ε	23	1,941.13	3.26	0.09
1	$S = \beta_0$ + Season + ε	20	1,942.58	4.70	0.05

[a] Estimate of overdispersion was 3.14. The analysis was conducted using a seasonal time step corresponding to spring (Apr–Jun), summer (Jul–Sep), autumn (Oct–Dec), and winter (Jan–Mar). Analysis was completed using the known-fates model with covariates in Program MARK with 1,064 individual records. Model variables include intercept (β_0), forest association (i.e., classification of each study site as oak–hickory or mixed-mesophytic forest association based on canopy tree species composition; Forest), temporal variation by season (Season), age of individual birds (i.e., juv or ad; Age), Gender of individual birds (Gender), and variance (ε).

[b] No. of estimated parameters in the model.

[c] Akaike's Information Criterion adjusted for small sample size and quasi-likelihood.

[d] AIC$_c$ differences.

[e] Akaike wt.

Survival 1998–1999.—The data set for 1998–1999 survival consisted of 328 individuals from MD-1, VA-1, VA-2, VA-3, WV-1, and WV-2. The global model had an estimated $\hat{C} = 2.068$ and the residuals were normally distributed. Model 2 had the greatest support ($w_i = 0.24$, Table 19) and indicated survival was a function of seasonal variation. Survival was highest in summer ($\bar{x} = 0.94$, 95% CI = 0.90–0.97), followed by winter ($\bar{x} = 0.84$, 95% CI = 0.77–0.89), autumn ($\bar{x} = 0.83$, 95% CI = 0.77–0.88), and spring ($\bar{x} = 0.76$, 95% CI = 0.68–0.82). Annual survival was 0.50 (95% CI = 0.36–0.62).

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

Model 14 also received moderate support and indicated survival was a function of forest association, age, gender, age × gender, MMNT$_{(\mathrm{win})}$, and SNOW (Table 19). Ruffed grouse in mixed-mesophytic forests had slightly higher survival ($\bar{x}$ difference = 0.01, 95% CI = 0.0–0.02) than grouse in oak–hickory forests, but the difference was not significant. Survival was negatively related to SNOW ($\beta_{\mathrm{logit}} = -0.164 \pm 0.063$, 95% CI = −0.295 to −0.04). Remaining explanatory factors in the model had confidence intervals that overlapped zero.

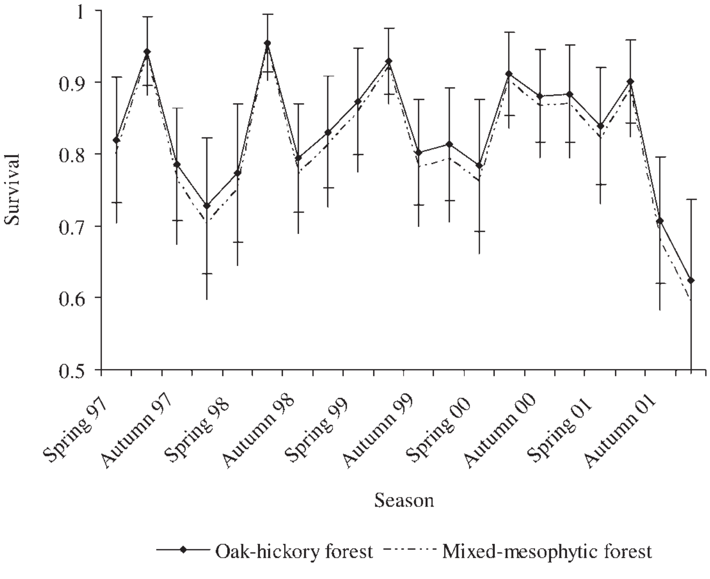

Figure 6. Ruffed grouse survival in oak–hickory and mixed-mesophytic forests in the southern and central Appalachian region, USA, 1997–2002. Estimates were generated using the known-fates with covariates model in Program MARK.

Survival 1999–2000.—The 1999–2000 survival data set consisted of 396 records and included data from MD-1, PA-1, VA-1, VA-2, VA-3, WV-1, and WV-2. The global model provided a good fit ($\hat{C} = 2.06$) with normally distributed residuals. Model 12 received the greatest support (Table 20) 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 oak–hickory forests ($\bar{x}$ difference = 0.07, 95% CI = 0.05–0.10) than in mixed-mesophytic forests (Table 21). Adult survival was slightly higher ($\bar{x}$ difference = 0.02, 95% CI = 0.00–0.04) but not different from juvenile survival. Survival was positively related to raptor abundance ($\beta_{\mathrm{Raptor}} = 0.24$, 95% CI = 0.07–0.41). Confidence intervals for the remaining parameters included zero.

Model 14 received moderate support (Table 20) and indicated survival was a function of forest association, age, gender, age × gender, SNOW, MMTN$_{(\mathrm{win})}$, and SNOW × MMTN$_{(\mathrm{win})}$. This model indicated ruffed grouse survival was higher in oak–hickory forests by 0.09 (95% CI = 0.06–0.13) than in mixed-mesophytic forests. Adult ruffed grouse survival was slightly higher ($\bar{x}$ difference = 0.02, 95% CI = 0.00–0.04), but not significantly different from juvenile survival. Survival was negatively related to

Table 18. A priori models and model selection results of ruffed grouse survival (S) in the southern and central Appalachian region, USA, 1997–1998.[a]

Model	Description	K[b]	QAIC$_c$[c]	Δ_i[d]	w_i[e]
2	$S = \beta_0$ + Season + ε	4	499.11	0.00	0.59
6	$S = \beta_0$ + Forest + Season + ε	6	502.04	2.93	0.14
5	$S = \beta_0$ + Gender + Season + ε	6	502.24	3.13	0.12
4	$S = \beta_0$ + Age + Season + ε	6	502.78	3.67	0.09

[a] Estimate of overdispersion was 2.45. Analysis was conducted using a seasonal time step corresponding to spring (Apr–Jun), summer (Jul–Sep), autumn (Oct–Dec), and winter (Jan–Mar). Model variables include intercept (β_0), forest association (i.e., classification of each study site as oak–hickory or mixed-mesophytic forest association based on canopy tree species composition; Forest), temporal variation by season (Season), age of individual birds (i.e., juv or ad; Age), gender of individual birds (Gender), and variance (ε).

[b] No. of estimated parameters in the model.

[c] Akaike's Information Criterion adjusted for small sample size and quasi-likelihood.

[d] AIC$_c$ differences.

[e] Akaike wt.

Table 19. A priori models and model selection results of ruffed grouse survival (S) in the southern and central Appalachian region, USA, 1998–1999.[a]

Model	Description	K[b]	QAIC$_c$[c]	Δ_i[d]	w_i[e]
2	$S = \beta_0 + \text{Season} + \varepsilon$	4	584.94	0.00	0.24
8	$S = \beta_0 + \text{Age} + \text{Gender} + \text{Age} \times \text{Gender} + \text{Season} + \varepsilon$	8	585.03	0.09	0.23
14	$S = \beta_0 + \text{Forest} + \text{Age} + \text{Gender} + \text{Age} \times \text{Gender} + \text{SNOW} + \text{MMNT}_{(\text{win})} + \text{SNOW} \times \text{MMNT}_{(\text{win})} + \text{Season} + \varepsilon$	12	585.37	0.43	0.20
4	$S = \beta_0 + \text{Age} + \text{Season} + \varepsilon$	6	585.42	0.48	0.19
5	$S = \beta_0 + \text{Gender} + \text{Season} + \varepsilon$	6	588.18	3.24	0.05

[a] Estimate of overdispersion was 2.07. Analysis was conducted using a seasonal time step corresponding to spring (Apr–Jun), summer (Jul–Sep), autumn (Oct–Dec), and winter (Jan–Mar). Model variables include intercept (β_0), forest association (i.e., classification of each study site as oak–hickory or mixed-mesophytic forest association based on canopy tree species composition; Forest), temporal variation by season (Season), age of individual birds (i.e., juv or ad; Age), gender of individual birds (Gender), $\bar{x}$ min. monthly temp in winter (MMNT$_{(\text{win})}$), mean no. of d with crusted snow during winter (SNOW), and variance (ε).

[b] No. of estimated parameters in the model.

[c] Akaike's Information Criterion adjusted for small sample size and quasi-likelihood.

[d] AIC$_c$ differences.

[e] Akaike wt.

Table 20. A priori models and model selection results of ruffed grouse survival (S) in the southern and central Appalachian region, USA, 1999–2000.[a]

Model	Description	K[b]	QAIC$_c$	Δ_i	w_i
12	$S = \beta_0 + \text{Forest} + \text{Age} + \text{Gender} + \text{Raptor} + \text{Prey} + \text{Raptor} \times \text{Prey} + \text{Season} + \varepsilon$	12	727.89	0.00	0.40
14	$S = \beta_0 + \text{Forest} + \text{Age} + \text{Gender} + \text{Age} \times \text{Gender} + \text{SNOW} + \text{MMNT}_{(\text{win})} + \text{SNOW} \times \text{MMNT}_{(\text{win})} + \text{Season} + \varepsilon$	12	729.26	1.37	0.20
6	$S = \beta_0 + \text{Forest} + \text{Season} + \varepsilon$	6	729.41	1.53	0.19
9	$S = \beta_0 + \text{Forest} + \text{Mast} + \text{Forest} \times \text{Mast} + \text{Season} + \varepsilon$	14	729.78	1.90	0.16

[a] The estimate of overdispersion was 2.06. Analysis was conducted using a seasonal time step corresponding to spring (Apr–Jun), summer (Jul–Sep), autumn (Oct–Dec), and winter (Jan–Mar). Model variables include intercept (β_0), forest association (i.e., classification of each study site as oak–hickory or mixed-mesophytic forest association based on canopy tree species composition; Forest), temporal variation by season (Season), age of individual birds (i.e., juv or ad; Age), gender of individual birds (Gender), $\bar{x}$ min. monthly temp in winter (MMNT$_{(\text{win})}$), the mean no. of Cooper's hawks and owls observed/hr by season (Raptor), the mean no. of rabbits and squirrels observed/hr by season (Prey), the mean no. of days with crusted snow during winter (SNOW), and variance (ε).

[b] No. of estimated parameters in the model.

[c] Akaike's Information Criterion adjusted for small sample size and quasi-likelihood.

[d] AIC$_c$ differences.

[e] Akaike wt.

MMNT$_{(\text{win})}$ ($\beta_{\text{MMNT(win)}} = -0.26$, 95% CI = -0.44 to -0.08). The remaining beta coefficients had confidence intervals that included zero.

Model 6 also received moderate support (Table 20) and indicated survival was a function of differences in forest association and seasonal variation (Table 21). Survival was highest in summer and lowest in autumn.

Table 21. Estimates of ruffed grouse seasonal survival rates in oak–hickory and mixed-mesophytic forests, USA, 1999–2000 in the southern and central Appalachian region, USA, based on 3 competing a priori models.[a]

		Forest association			
		Oak–hickory		Mixed-mesophytic	
Model	Season	$\bar{x}$	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
	Autumn	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
	Autumn	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
	Autumn	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

[a] Analysis was conducted using a seasonal time step corresponding to spring (Apr–Jun), summer (Jul–Sep), autumn (Oct–Dec), and winter (Jan–Mar).

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

Survival 2000–2001.—The 2000–2001 survival data set included 327 records including data from MD-1, PA-1, VA-1, WV-1, and WV-2. 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 22). This model was 4.3 times more likely to be the best model than the next competing model. Ruffed grouse in oak–hickory forests had higher survival than grouse in mixed-mesophytic forests (Table 23). Seasonal survival was highest in summer and lowest in spring on oak–hickory and mixed-mesophytic forests. Parameter estimates for the influence of mast production during each season included zero.

Survival 2001–2002.—The final data set for 2001–2002 consisted of 219 records from KY-1, PA-1, VA-2, and WV-2. The estimate of overdispersion for the global model was 2.025 and the residuals were normally distributed. Our best model indicated survival varied by season (Table 24). Survival was highest in the summer ($\bar{x} = 0.93$, 95% CI = 0.85–0.97), followed by spring ($\bar{x} = 0.92$, 95% CI = 0.83–0.96), winter ($\bar{x} = 0.83$, 95% CI = 0.72–0.90), and autumn ($\bar{x} = 0.74$, 95% CI = 0.64–0.81). Annual survival was 0.53 (95% CI = 0.33–0.68). This model had a 39% probability of being the best model, but was only 1.22 times more

Table 22. A priori models and model selection results of ruffed grouse survival (S) in the southern and central Appalachian region, USA, 2000–2001.[a]

Model	Description	K[b]	QAIC$_c$[c]	Δ_i[d]	w_i[e]
9	$S = \beta_0 + \text{Forest} + \text{Mast} + \text{Forest} \times \text{Mast} + \text{Season} + \varepsilon$	14	592.49	0.00	0.65
6	$S = \beta_0 + \text{Forest} + \text{Season} + \varepsilon$	6	595.37	2.88	0.15
10	$S = \beta_0 + \text{Forest} + \text{Mast} + \text{Age} + \text{Gender} + \text{Age} \times \text{Gender} + \text{Season} + \varepsilon$	13	596.43	3.94	0.09

[a] Estimate of overdispersion was 1.94. Analysis was conducted using a seasonal time step corresponding to spring (Apr–Jun), summer (Jul–Sep), autumn (Oct–Dec), and winter (Jan–Mar). Model variables include intercept (β_0), forest association (i.e., classification of each study site as oak–hickory or mixed-mesophytic forest association based on canopy tree species composition; Forest), index of annual hard mast production (Mast), temporal variation by season (Season), age of individual birds (i.e., juv or ad; Age), gender of individual birds (Gender), and variance (ε).

[b] No. of estimated parameters in the model.

[c] Akaike's Information Criterion adjusted for small sample size and quasi-likelihood.

[d] AIC$_c$ differences.

[e] Akaike wt.

likely to be the best model than the next competing model (Table 24).

Model 6 received moderate support (Table 24) 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 oak–hickory forests ($\bar{x}$ difference = 0.04, 95% CI = 0.02–0.05) than in mixed-mesophytic forests.

Autumn survival.—The final autumn survival data set included 1,006 records and included data from KY-1, MD-1, PA-1, RI-1, VA-1, VA-2, VA-3, WV-1, and WV-2. The global model provided adequate fit with normal residuals and $\hat{C} = 1.35$. The best model (model 14, Table 25) 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 autumn survival was a function of study area, year, time (i.e., month), and age. Adult grouse had higher survival ($\bar{x}$ difference = 0.02, 95% CI = 0.01–0.03) than juveniles in the autumn. Remaining explanatory factors in this model had 95% confidence intervals that overlapped zero.

Winter survival.—The winter survival data set consisted of 876 records including data from KY-1, MD-1, PA-1, RI-1, VA-1, VA-2, VA-3, WV-1, and WV-2. 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 26). 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% CI = 0.05–0.31). The confidence interval of the effect of age overlapped zero, indicating a weak or nonexisting effect on survival.

Table 23. Ruffed grouse seasonal and annual survival rates in oak–hickory and mixed-mesophytic forests in the southern and central Appalachian region, USA, using model 9, April 2000–March 2001.

	Forest association			
	Oak–hickory		Mixed-mesophytic	
Season	$\bar{x}$	95% CI	$\bar{x}$	95% CI
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
Autumn	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

Model 9 provided similar results as model 5 and indicated winter survival was a function of age, gender, age × gender, 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 ($\beta_{\text{cloglog}} = 0.04 \pm 0.014$, 95% CI = 0.01–0.07). Confidence intervals of the beta estimates for the influence of gender and the presence of an interaction included zero.

Spring survival.—The final spring survival data set consisted of 841 records from KY-1, MD-1, PA-1, RI-1, VA-1, VA-2, VA-3, WV-1, and WV-2. The estimate of over dispersion was low ($\hat{C} = 1.35$) and the residuals were normally distributed. Model 6 received the greatest support (Table 27) 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 gender, year, and month. Males had higher survival than females (Table 28). Models 18 and 10 received limited to moderate support ($\Delta_i \leq 1.75$) and produced nearly identical survival estimates as model 6 (Devers 2005). 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 KY-1, MD-1, PA-1, RI-1, VA-1, VA-2, VA-3, WV-1, and WV-2. The global model

Table 24. A priori models and model selection results of ruffed grouse survival (S) in the southern and central Appalachian region, USA, 2001–2002.[a]

Model	Description	K[b]	QAIC$_c$[c]	Δ_i[d]	w_i[e]
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	$S = \beta_0 + \text{Age} + \text{Gender} + \text{Age} \times \text{Gender} + \text{Season} + \varepsilon$	8	281.72	2.92	0.09
4	$S = \beta_0 + \text{Age} + \text{Season} + \varepsilon$	6	282.76	3.96	0.05
5	$S = \beta_0 + \text{Gender} + \text{Season} + \varepsilon$	6	282.83	4.04	0.05

[a] Estimate of overdispersion was 2.09. Analysis was conducted using a seasonal time step corresponding to spring (Apr–Jun), summer (Jul–Sep), autumn (Oct–Dec), and winter (Jan–Mar). Model variables include intercept (β_0), forest association (i.e., classification of each study site as oak–hickory or mixed-mesophytic forest association based on canopy tree species composition; Forest), temporal variation by season (Season), age of individual birds (i.e., juv or ad; Age), gender of individual birds (Gender), and variance (ε).

[b] No. of estimated parameters in the model.

[c] Akaike's Information Criterion adjusted for small sample size and quasi-likelihood.

[d] AIC$_c$ differences.

[e] Akaike wt.

Table 25. A priori models and results of model selection process of ruffed grouse survival (S) during autumn (Oct–Dec) in the southern and central Appalachian region, USA, 1996–2001.[a]

Model	Description	K[b]	QAIC$_c$[c]	Δ_i[d]	w_i[e]
14	$S = \beta_0 + SA + Age + Gender + Age \times Gender + YR + Month + \varepsilon$ (cloglog)	19	1,789.18	0.00	0.60
5	$S = \beta_0 + Age + YR + Month + \varepsilon$	9	1,791.57	2.38	0.18
9	$S = \beta_0 + Age + Gender + Age \times Gender + YR + Month + \varepsilon$	11	1,791.59	2.41	0.18

[a] Estimate of overdispersion was 1.35. Analysis was conducted using a monthly time step. Model variables include intercept (β_0), study area (SA), temporal variation by yr (YR), temporal variation by month (Month), age of individual birds (i.e., juv or ad; Age), gender of individual birds (Gender), and variance (ε).

[b] No. of estimated parameters in the model.

[c] Akaike's Information Criterion adjusted for small sample size and quasi-likelihood.

[d] AIC$_c$ differences.

[e] Akaike wt.

Table 26. A priori models and results of model selection process of ruffed grouse survival (S) during winter (Jan–Mar) in the southern and central Appalachian region, USA, 1997–2002.[a]

Model	Description	K[b]	QAIC$_c$[c]	Δ_i[d]	w_i[e]
5	$S = \beta_0 + Age + YR + Month + \varepsilon$ (cloglog)	9	1517.44	0.00	0.41
9	$S = \beta_0 + Age + Gender + Age \times Gender + YR + Month + \varepsilon$ (cloglog)	11	1518.35	0.91	0.26
7	$S = \beta_0 + Forest + YR + Month + \varepsilon$ (cloglog)	9	1519.21	1.77	0.17
6	$S = \beta_0 + Gender + YR + Month + \varepsilon$	9	1519.26	1.82	0.16

[a] Estimate of overdispersion was 1.37. Analysis was conducted using a monthly time step. Model variables include intercept (β_0), temporal variation by yr (YR), temporal variation by month (Month), age of individual birds (i.e., juvenile or adult; Age), gender of individual birds (Gender), forest association (i.e., classification of each study site as oak–hickory or mixed-mesophytic forest association based on canopy tree species composition; Forest), and variance (ε).

[b] No. of estimated parameters in the model.

[c] Akaike's Information Criterion adjusted for small sample size and quasi-likelihood.

[d] AIC$_c$ differences.

[e] Akaike wt.

provided an adequate fit ($\hat{C} = 0.60$). Only 2 models (7 and 8) were supported as competing models (Table 29). The best model (model 7) indicated survival was influenced by forest, year, and month (Table 30). 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, gender, year, and time. This model indicated survival varied by year and month, but the confidence interval for gender overlapped zero. Survival estimates were identical to those produced by model 7 (Devers 2005). Mean survival in July, averaged across the 2 competing models, was 0.96 ± 0.0, 0.98 ± 0.0 in August, and 0.96 ± 0.0 in September. In summary, forest association, time, age, and gender influenced ruffed grouse survival. Ruffed grouse survival was higher in oak–hickory forests than in mixed-mesophytic forests and was highest in summer and lowest in winter. The influence of age and gender on ruffed grouse survival was equivocal.

Test of the Compensatory Mortality Hypothesis

Hunters harvested 117 radiomarked birds (including legal harvest, crippling loss, and illegal harvest) between autumn 1996 and autumn 2001. Harvest mortality accounted for 4–30% of all known mortalities on the 7 study areas (Table 31). Hunters harvested birds during each month of the hunting season (Table 32) and one bird was illegally harvested in March. Annual survival (pooled across gender and age classes) did not differ between hunted and nonhunted groups, by phase or year (nested in phase), nor was there evidence of an interaction between treatment and phase or treatment and year (nested with phase; Table 33, Fig. 7). During Phase I (autumn 1996 to summer 1999) hunting was open on all study areas. We closed ruffed grouse hunting on the 3 treatment areas during Phase II (autumn 1999 to summer 2003). Comparison of annual survival rates across treatment study areas indicated variable responses to the closure of hunting (Fig. 8). There was no evidence of a treatment × year (nested within phase)

Table 27. A priori models and results of model selection process of ruffed grouse survival (S) during spring (Apr–Jun) in the southern and central Appalachian region, USA, 1997–2002.[a]

Model	Description	K[b]	QAIC$_c$[c]	Δ_i[d]	w_i[e]
6	$S = \beta_0 + Gender + YR + Month + \varepsilon$	9	1,587.30	0.00	0.42
18	$S = \beta_0 + Age + Gender + YR + Month + \varepsilon$ (cloglog)	10	1,587.60	0.30	0.36
10	$S = \beta_0 + Age + Gender + Age \times Gender + YR + Month + \varepsilon$ (cloglog)	11	1,589.04	1.75	0.18

[a] Estimate of overdispersion was 1.35. Analysis was conducted using a monthly time step. Model variables include intercept (β_0), temporal variation by yr (YR), temporal variation by month (Month), age of individual birds (i.e., juv or ad; Age), gender of individual birds (Gender), and variance (ε).

[b] No. of estimated parameters in the model.

[c] Akaike's Information Criterion adjusted for small sample size and quasi-likelihood.

[d] AIC$_c$ differences.

[e] Akaike wt.

Table 28. Estimates of male and female monthly survival rates during spring in the southern and central Appalachian region, USA, 1997–2000 based on model 6.

		F		M	
Yr	Season	$\bar{x}$	95% CI	$\bar{x}$	95% CI
1997	Apr	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
	Jun	0.97	0.96–0.98	0.98	0.97–0.98
1998	Apr	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
	Jun	0.98	0.97–0.98	0.98	0.98–0.99
1999	Apr	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
	Jun	0.97	0.96–0.98	0.98	0.97–0.98
2000	Apr	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
	Jun	0.98	0.97–0.98	0.99	0.98–1.0

Table 30. Estimates of ruffed grouse monthly summer survival by forest association (oak–hickory and mixed-mesophytic) in the southern and central Appalachian region, USA, 1997–2001 based on model 7.

		Forest association			
		Oak–hickory		Mixed-mesophytic	
Yr	Month	$\bar{x}$	95% CI	$\bar{x}$	95% CI
1997	Jul	0.96	0.95–0.97	0.95	0.93–0.97
	Aug	0.98	0.97–0.99	0.98	0.97–0.99
	Sep	0.96	0.92–0.98	0.95	0.89–0.98
1998	Jul	0.96	0.94–0.97	0.95	0.92–0.96
	Aug	0.98	0.97–0.99	0.98	0.96–0.99
	Sep	0.96	0.91–0.98	0.94	0.87–0.97
1999	Jul	0.96	0.94–0.97	0.94	0.91–0.96
	Aug	0.98	0.97–0.99	0.97	0.95–0.98
	Sep	0.95	0.90–0.98	0.94	0.86–0.97
2000	Jul	0.96	0.94–0.97	0.94	0.92–0.96
	Aug	0.98	0.97–0.99	0.97	0.96–0.99
	Sep	0.96	0.90–0.98	0.94	0.87–0.97
2001	Jul	0.96	0.94–0.97	0.94	0.92–0.96
	Aug	0.98	0.97–0.99	0.97	0.96–0.98
	Sep	0.96	0.91–0.98	0.94	0.87–0.87

interaction for adult annual survival ($F_{3,18.6} = 1.37$, $P = 0.282$), 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 ($F_{3,17.9} = 0.29$, $P = 0.831$). We found no evidence of treatment × phase interactions for nest rate ($F_{1,24} = 0.07$, $P = 0.797$), nest success ($F_{1,21.5} = 1.97$, $P = 0.175$), hatching success ($F_{1,21.5} = 1.16$, $P = 0.294$), or chick survival to 35 days posthatch ($F_{1,22.9} = 2.63$, $P = 0.119$).

The mean harvest rate on control sites between 1996 and 2001 was 0.08 ± 0.0017 (95% CI = 0.05–0.12). The mean harvest rate on treatment sites from 1996 to 1999 was 0.20 ± 0.0. 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. 9). Estimates of harvest rates included illegal harvest and did not equal zero in all years on the treatment sites.

Population Modeling

The objective of our deterministic modeling procedure was to estimate λ and 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 constant across spatial scales (Table 34) and were used in all 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 35).

Elasticity analyses indicated chick survival (model 1, Fig. 10) and fecundity (model 2, Fig. 11) had the greatest influence on λ. Winter and autumn survival had relatively moderate influence on λ in each model (Figs. 10, 11). The influence of mast production the previous autumn on chick survival (i.e., the influence of mast, model 1, Fig. 10) and on fecundity (i.e., model 2, Fig. 11) had less influence on λ.

DISCUSSION

Reproductive Analysis

Regional comparison of reproductive parameters.—Mean nesting rate was 100% and 86% in mixed-mesophytic and oak–hickory forests, respectively. Our estimate of nesting rate in mixed-mesophytic forests was similar to rates reported in the core of the species' range. In contrast, the mean nesting rate in oak–hickory

Table 29. A priori models and results of model selection process of ruffed grouse survival (S) during summer (Jul–Sep) in the southern and central Appalachian region, USA, 1997–2002.[a]

Model	Description	K^b	$QAIC_c^c$	Δ_i^d	w_i^e
7	$S = \beta_0 + \text{Forest} + \text{YR} + \text{Month} + \varepsilon$	10	1,355.78	0.00	0.55
8	$S = \beta_0 + \text{Forest} + \text{Gender} + \text{YR} + \text{Month} + \varepsilon$	11	1,357.73	1.95	0.21
13	$S = \beta_0 + \text{Forest} + \text{Raptor} + \text{Prey} + \text{Raptor} \times \text{Prey} + \text{Month} + \varepsilon$	8	1,358.51	2.73	0.14
10	$S = \beta_0 + \text{Forest} + \text{Gender} + \text{Forest} \times \text{Gender} + \text{Month} + \varepsilon$	12	1,359.65	3.87	0.08
5	$S = \beta_0 + \text{Gender} + \text{YR} + \text{Month} + \varepsilon$	9	1,364.96	9.18	0.01
4	$S = \beta_0 + \text{YR} + \text{Month} + \varepsilon$	9	1,365.26	9.48	0.00
2	$S = \beta_0 + \text{Month} + \varepsilon$	3	1,365.70	9.92	0.00

[a] Estimate of overdispersion was 0.60. Analysis was conducted using a monthly time step. Model variables include intercept (β_0), forest association (i.e., classification of each study site as oak–hickory or mixed-mesophytic forest association based on canopy tree species composition; Forest), temporal variation by yr (YR), temporal variation by month (Month), gender of individual birds (Gender), $\bar{x}$ min. monthly temp in winter ($MMNT_{(win)}$), the mean no. of Cooper's hawks and owls observed/hr by season (Raptor), the mean no. of rabbits and squirrels observed/hr by season (Prey), and variance (ε).

[b] No. estimated parameters in the model.

[c] Akaike's Information Criterion adjusted for small sample size and quasi-likelihood.

[d] AIC_c differences.

[e] Akaike wt.

Table 31. Mean harvest rates of ruffed grouse on 7 study areas in the southern and central Appalachian region, USA, participating in a test of the compensatory mortality hypothesis, 1997–2001.

Study area	n	Known mortalities			Harvest rate		
		% harvest	SD	95% CI	$\bar{x}$	SD	95% CI
KY-1	2	0.30	0.078	0.0–0.99	0.37	0.191	0.0–1.0
MD-1	5	0.11	0.060	0.03–0.18	0.14	0.075	0.05–0.23
VA-1	4	0.11	0.087	0.0–0.24	0.23	0.169	0.0–0.50
VA-2	5	0.05	0.048	0.0–0.11	0.11	0.078	0.0–0.20
VA-3	2	0.16	0.035	0.0–0.47	0.21	0.014	0.08–0.34
WV-1	5	0.04	0.054	0.0–0.11	0.06	0.084	0.0–0.17
WV-2	2	0.16	0.064	0.0–0.073	0.21	0.092	0.0–1.0

Table 33. Repeated measures analysis of variance test of the effects of hunting on ruffed grouse annual survival (Apr–Mar) pooled across age and gender classes in the southern and central Appalachian region, USA, 1996–2002.[a]

Source	Numerator df	Denominator df	F	P
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 × yr(phase)	3	18.4	0.22	0.884

[a] Analysis was conducted using Proc Mixed (SAS Institute 2000). Phase I was spring 1997–summer of 1999 during which control and treatment sites were open to hunting. Phase II was autumn 1999–summer 2002 during which treatment sites were closed to hunting.

forests was lower than previously reported. Most females of all forest grouse species attempt to nest each year (Bergerud and Gratson 1988). During the course of their study in New York, Bump et al. (1947) reported 100% nesting rate during 7 of 10 years, but estimated nesting rate may have been as low as 75% in some years; they concluded nonnesting was a minor factor in ruffed grouse productivity. Nesting rate in Michigan was 65%, but all females probably attempted to nest each year (Larson 1998). Several researchers working throughout Wisconsin reported 100% nesting rate (Holzwart 1990, Balzer 1995, Small et al. 1996).

The mean start of incubation during our study was 28 April and 2 May for adult and juvenile females, respectively. 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 (approx. 24 d; Bump et. al 1947), therefore, incubation and hatching dates are correlated. Peak hatching occurred during the last week of May in northeastern Iowa, USA (Porath and Vohs 1972); the last week of May and first week of June in New York, USA (Bump et al. 1947), Wisconsin, USA (Hale and Wendt 1951, Maxon 1978), and Ontario, Canada (Cringan 1970); and between the first and third week of June in Minnesota, USA (Kupa 1966).

Mean clutch size was 9.4 and 10.4 eggs in oak–hickory and mixed-mesophytic forest, respectively. Our estimate of mean clutch size in oak–hickory forests is lower than previously reported in the central portion of the species range. Mean clutch size in mixed-mesophytic 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 to 12.2 eggs (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 oak–hickory forests.

Median hatching success in the Appalachian region was 82% and was similar to most reported estimates of hatching success throughout ruffed grouse range. In New York, estimates of mean hatching success ranged from 95% (Bump et al. 1947) to 97% (Edminster 1947). Researchers in Canada reported mean hatching success rates from 87% in Ontario (Cringan 1970) to 97% in Alberta (Rusch and Keith 1971). Early studies conducted in Minnesota reported hatching success ranged from 59% to 68% (Marshall and Gullion 1965, Maxon 1978), but these studies may provide inaccurate estimates because they did not incorporate radiomarked females. We conclude the poor fit of our models was due to the relatively low variation in hatching success across individuals, study areas, forest associations, and years. Bump et al. (1947) commented on the lack of variation in hatching success (or egg fertility) and concluded losses from failed eggs (or embryonic death) had a minor role in grouse dynamics relative to other aspects of productivity and mortality. Our findings and those of

Table 32. Distribution of hunter harvested (including legal harvest, crippling loss, and illegal harvest) radiomarked birds (pooled across yr) on study areas in the southern and central Appalachian region, USA, to test the compensatory mortality hypothesis, 1997–2001.[a]

Month	No. harvested	% total harvest
Oct	26	22
Nov	30	26
Dec	14	12
Jan	23	20
Feb	23	20
Mar	1	<1.0

[a] Information on harvested birds was obtained through the use of a reward system. Information on illegal harvest and crippling loss was obtained through inspection of remains and law enforcement efforts.

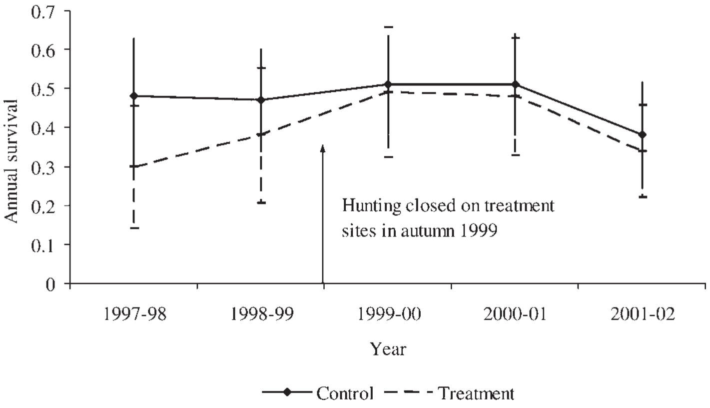

Figure 7. Ruffed grouse annual survival (pooled across gender and age class) on treatment and control sites in the southern and central Appalachian region, USA, 1997–2002. Treatment sites were open to hunting from 1996 to 1998 (Phase I) and closed to hunting from 1999 to 2001 (Phase II). Control sites were open to hunting every year. Estimates were obtained using the known-fates model in Program MARK.

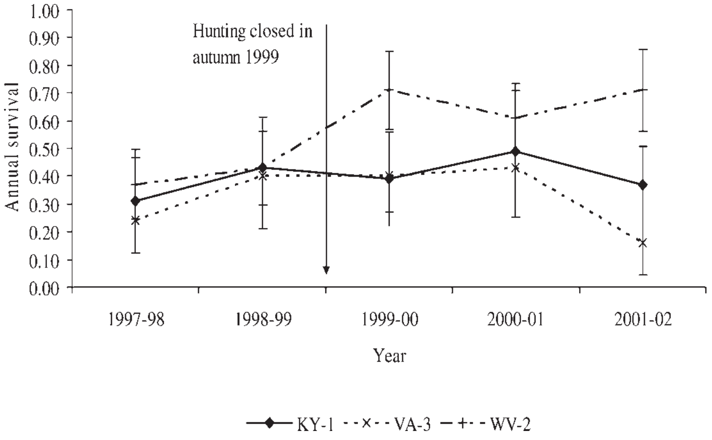

Figure 8. Ruffed grouse annual survival (pooled across gender and age class) on 3 treatment sites in the southern and central Appalachian region, USA, 1997–2002. Treatment sites were open to hunting from 1996 to 1998 (Phase I) and closed to hunting from 1999 to 2001 (Phase II). Estimates were obtained using the known-fates model in Program MARK.

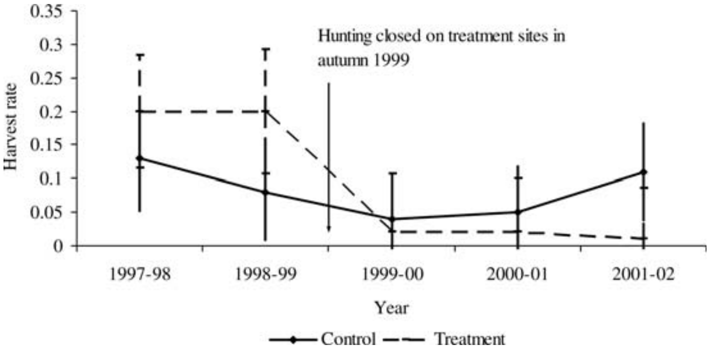

Figure 9. Ruffed grouse harvest rates on control and treatment sites in the southern and central Appalachian region, USA, 1997–2002. Treatment sites were open to hunting from 1996 to 1998 (Phase I) and closed to hunting from 1999 to 2001 (Phase II). Estimates were obtained using the known-fates model in Program MARK.

other researchers (Edminster 1947, Cringan 1970, Rusch and Keith 1971, Balzer 1995) support this conclusion.

Mean nest success in the Appalachian region (63% and 70% in oak–hickory and mixed-mesophytic 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). Mean nest success in the Appalachian region was higher than rates reported in Wisconsin (43–48%; Holzwart 1990, Balzer 1995, Small et al. 1996) and Michigan (48%; Larson 1998).

Ruffed grouse renesting rate, similar to nesting rate, differed substantially between oak–hickory (3%) and mixed-mesophytic (45%) forests. Renesting rate on mixed-mesophytic forests was within the range of those reported throughout ruffed grouse range. Renesting rate was 22–26% in New York (Bump et al. 1947), 46% in Michigan, USA (Larson 1998), 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 females with failed first nests attempt a second nest. The most similar renesting rate to our estimate of 3% renesting in oak–hickory forests was 14% in Minnesota (Maxon 1978).

Female success is seldom reported in ruffed grouse research, probably due to the minor contribution of renesting to ruffed grouse productivity (Bump et al. 1947). In the Appalachian region, mean female success ranged from 63% in oak–hickory forests to 70% in mixed-mesophytic forests.

Compared to other portions of ruffed grouse range, chick survival to 35 days posthatch (22%) in the Appalachian region was extremely low. Using radiomarked chicks, Smith et al. (2004) estimated ruffed grouse chick survival to 35 days posthatch was 6%. Chick survival to brood break up (approx. 82 d) 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 ($\geq$77 d) was 40% (Bump et al. 1947). Chick survival to 56 days posthatch in Ontario was 78% (Beckerton and Middleton 1982). 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 and probably overestimated chick survival. In a recent study in Michigan, researchers placed radiotransmitters on 6-day-old chicks and estimated survival during a 12-week period was 32% (Larson et al. 2001). Their 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).

Factors influencing reproduction.—Difference in forest associations and variation in annual hard mast production were the primary influences on ruffed grouse reproduction. Ruffed grouse productivity was lower in oak–hickory than mixed-mesophytic forests and was positively related to hard mast production regardless of forest association. We believe the primary difference between oak–hickory and mixed-mesophytic forest is the quality and availability of food resources. Previous research has demonstrated that ruffed grouse diets in the Appalachian region compared to the Great Lakes region are lower in metabolizable energy and crude protein, and higher in total phenols and tannins (Norman and Kirkpatrick 1984, Servello and Kirkpatrick 1987). Although the authors did not identify their study areas as oak–hickory forest associations, these studies were conducted in western Virginia in areas dominated by oak and hickory. Further, ruffed grouse in the Appalachians rely heavily on hard mast production, including acorns and beechnuts (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 with insufficient endogenous reserves (Long et al. 2004*a*) resulting in lower reproductive effort and success. In contrast, grouse in mixed-mesophytic forests do not experience the same nutritional limitations because they have access to high quality food items, specifically the buds and catkins of cherries, birch and, in Pennsylvania, USA, aspen. The presence of these food resources allow grouse in mixed-mesophytic forests to maintain sufficient endogenous reserves resulting in higher reproductive effort and

Table 34. Stable age distributions used in development of deterministic models of ruffed grouse population growth in the southern and central Appalachian region, USA, 1996–2002.[a]

	Model 1				Model 2			
Spatial scale	**Age 1**	**Age 2**	**Age 3**	**Age 4**	**Age 1**	**Age 2**	**Age 3**	**Age 4**
Regional[b]	0.492	0.273	0.151	0.084	0.570	0.259	0.118	0.054
Mixed-mesophytic forests[c]	0.511	0.271	0.143	0.076	0.555	0.262	0.124	0.059
Oak–hickory forests[c]	0.432	0.277	0.177	0.113	0.554	0.263	0.124	0.059
Mixed-mesophytic study area[d]	0.532	0.267	0.134	0.067	0.575	0.258	0.115	0.052
Oak–hickory study area[d]	0.447	0.276	0.171	0.106	0.555	0.262	0.124	0.059

[a] Model 1 incorporated multiple variables including nest rate (proportion of F that attempted to nest), nest success (proportion of nests from which ≥1 egg hatched), renest rate (proportion of F with a failed first nest that attempted a second nest), clutch size ($\bar{x}$ no. of eggs laid/nest), hatching success (proportion of eggs from a successful first nest that hatched), and chick survival to 35 d posthatch to estimate productivity. Model 2 and estimated productivity with one parameter, the $\bar{x}$ no. of chicks produced at 35 d posthatch per F alive on 1 Apr.

[b] Parameter estimates at the regional scale were calculated pooling across all study areas and averaging across yr.

[c] 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 yr.

[d] Parameter estimates for mixed-mesophytic and oak–hickory forest study areas were calculated by averaging across yr and study areas identified as dominated by respective forest type.

success. For example, following an extremely poor mast crop in autumn 1997 on the VA-1 study area, none of 6 radiomarked females nested in spring 1998. In contrast, we did not document complete failure of nesting during any year on any of the mixed-mesophytic forest study areas. Our results indicated a weak, but positive relationship ($R^2 = 0.04$) between chick survival and hard mast production the previous autumn. Given the coarseness of our mast evaluation procedure, we believe our results indicate autumn mast production (mediated through F condition) is one mechanism influencing chick survival in the Appalachian region. Complementary research conducted as part of the ACGRP showed percent carcass fat of female ruffed grouse was positively related to mast production in autumn and the presence of acorns in the crop in late winter (Long et al. 2004*b*). Additionally, chick survival to 35 days posthatch was positively correlated with the amount of carcass fat in females (Long et al. 2004*a*). Study areas where females had low mean fat levels had lower chick survival rates to 35 days posthatch (13%) compared to areas with moderate (37%) and high (26%) fat levels (Long et al. 2004*a*).

Nutrition and female condition influence reproduction in many avian species (Martin 1987, Jakubas et al. 1993, Nager et al. 2000, Reynolds et al. 2003, Verboven 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. In a review of the influence of habitat quality on gamebird ecology, Rands (1988) concluded variation in willow ptarmigan (*Lagopus lagopus*) productivity was due to variation in the quality of food available to the female. He also concluded maternal nutrition might limit grouse and ptarmigan productivity through influencing multiple aspects of reproduction including nesting rate, clutch size, renest rate, and chick survival. In a study of capercaillie (*Tetrao urogallus*) 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

Table 35. Estimates of ruffed grouse finite population growth rate (λ) and fecundity (F and F') in the southern and central Appalachian region, USA, 1996–2002 based on 2 alternative deterministic models at 3 spatial scales.[a]

	Model 1		Model 2	
Scale	**λ**	**F**	**λ**	**F'**
Regional[b]	0.78	0.66	0.95	0.92
Mixed-mesophytic forests[c]	0.73	0.69	0.82	0.84
Oak–hickory forests[c]	0.79	0.53	1.06	0.91
Mixed-mesophytic study area[d]	0.72	0.73	0.81	0.89
Oak–hickory study area[d]	0.74	0.54	1.04	0.87

[a] Model 1 estimated F as a function of multiple reproductive parameters nest rate (proportion of F that attempted to nest), nest success (proportion of nests from which ≥1 egg hatched), renest rate (proportion of F with a failed first nest that attempted a second nest), clutch size ($\bar{x}$ no. of eggs laid/nest), hatching success (proportion of eggs from a successful first nest that hatched), and chick survival to 35 d posthatch. Model 2 estimated F' using one parameter (no. of chicks alive at 35 d posthatch/F alive on 1 Apr). Models were developed using population vital rates estimated from data collected during the Appalachian Cooperative Grouse Research Project, 1996–2002.

[b] Parameter estimates at the regional scale were calculated pooling across all study areas and averaging across yr.

[c] 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 yr.

[d] Parameter estimates for mixed-mesophytic and oak–hickory forest study areas were calculated by averaging across yr and study areas identified dominated by the respective forest type.

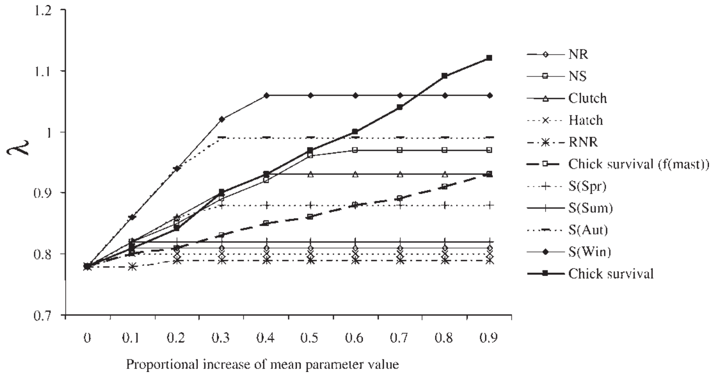

Figure 10. Elasticity analysis of ruffed grouse finite growth rate in the southern and central Appalachian region, USA, based on deterministic model 1. This model used multiple parameters (i.e., nesting rate, nest success, clutch size, and hatching success) to estimate productivity.

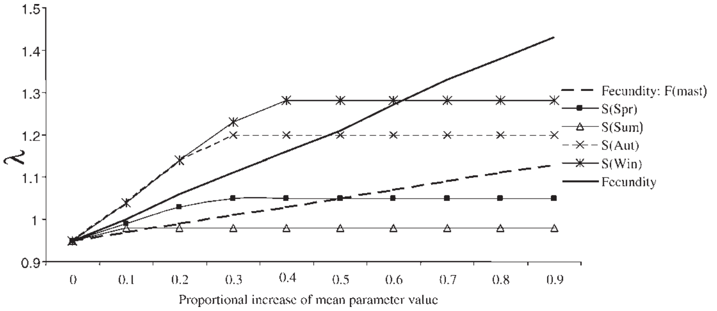

Figure 11. Elasticity analysis of ruffed grouse finite population growth rate in the southern and central Appalachian region, USA, based on model 2. Model 2 estimated productivity using 1 parameter (no. chicks alive at 35 days posthatch/F alive on 1 Apr).

ratio in their diet (Beckerton and Middleton 1982). Several studies of red grouse (*L. lagopus lagopus*) in Europe have correlated productivity with nutritional quality (Moss 1969, 1972; Watson et al. 1984). Further, experimental studies have demonstrated red grouse productivity is higher in areas with higher quality heather (*Calluna vulgaris*; Miller et al. 1970, Watson et al. 1984).

Female nutritional condition is one of 2 primary factors, the other being the availability of insects for newly hatched chicks, which influences gamebird chick survival (Dobson et al. 1988). Researchers working with multiple species of tetraonids have drawn similar conclusions (Jenkins et al. 1967, Moss 1969, Miller et al. 1970, Watson and O'Hare 1979, Hewitt and Kirkpatrick 1996). Red grouse feed selectively on portions of heather that are rich in nitrogen and phosphorus (Moss 1972, Lance 1983) and have higher productivity in 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 adult female nutritional condition influences egg quality and chick viability (i.e., survival). Females in good nutritional condition lay higher quality eggs with larger yolks and greater energy reserves for newly hatched chicks. The amount of yolk available to newly hatched grouse and ptarmigan chicks is critical because chicks cannot thermoregulate for the first 7 days posthatch (Moss et al. 1981, Williams 1994). During periods of inclement weather, chicks must be brooded by the female and rely on yolk reserves to meet their energy requirements.

In his review of food as a limiting factor in avian reproduction, Martin (1987) argued the reproductive strategy of a population should reflect evolutionary selection. Further, in ecological time, responses in reproductive effort should vary around the mean life-history strategy with variation in food availability and quality. This variation is expressed in the physiological condition of the parent at the beginning of the reproductive season and reproductive effort exerted by the individual. In years of low food availability, females experience decreases in endogenous reserves and must either decrease investment in the current offspring (i.e., fewer or lower quality) or increased dependence on exogenous resources, which takes time and energy from caring for the young (i.e., brooding). Under these conditions birds may maximize the number of surviving young by responding with ≥1 of the following strategies: 1) increasing clutch size at the cost of decreasing individual egg quality; 2) increasing egg quality by decreasing reserves for themselves or energy for young during future stages of reproduction (i.e., incubation or brooding); 3) increasing individual egg quality by delaying initiation of egg laying and reducing the ability to renest; or 4) forgoing breeding in the current season and invest energy in survival and future reproductive efforts. Ruffed grouse life history strategy in oak–hickory forests of the central and southern Appalachians appear to have evolved for lower reproductive effort (relative to mixed-mesophytic forests and the northern hardwoods of the Great Lakes region) in response to nutritional limitation. Further, during years of poor hard mast production, ruffed grouse may forgo breeding and invest endogenous reserves into survival and future breeding attempts. Finally, in springs following poor mast production, chick survival is low (regardless of environmental conditions) due to poor egg quality and weak chicks. In springs following above average mast production, chick survival increases, presumably because larger chicks are produced with a greater amount of energy reserves in the form of remaining yolk. In springs following average mast production, we believe other environmental factors (i.e., temp and precipitation) have greater influence on chick survival (Healy and Nenno 1985, Vangilder and Kurzejeski 1995, Roberts and Porter 1998).

Age and latitude also influenced ruffed grouse reproduction. In our study, adult females initiated incubation earlier than juveniles. Earlier incubation in adults is common among tetraonid species. Adult ruffed grouse in Minnesota initiated incubation approximately 2 days earlier then 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). Bergerud (1988) hypothesized that grouse should initiate nesting as early as possible (without increasing the risk of nest predation) to provide an opportunity to renest (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 and establishing nest sites, or because they are in better physical condition than first time nesters.

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; 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 (Devers 2005). 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 (Devers 2005).

Survival Analysis

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

Table 36. Factors (X) identified to have influenced ruffed grouse survival in the southern and central Appalachian region, USA, 1996–2002 using information theoretic model selection.[a]

Factor	Model set									
	5-yr	1997–1998	1998–1999	1999–2000	2000–2001	2001–2002	Spring	Summer	Autumn	Winter
Season	X	X	X	X	X	X	—	—	—	—
Month	—	—	—	—	—	—	—	X	X	X
YR	—	—	—	—	—	—	X	X	X	X
Forest	X			X	X	X		X		
Age								—	X	X
Gender							X			
SNOW	—		X				—	—		
Raptor	—									
$\mathrm{MMNT}_{(\mathrm{win})}$				X						
Study area									X	

[a] Factors were in top competing models (i.e., models with $\Delta_i \approx 2.0$) and had beta coeff. with 95% CIs that did not overlap zero. Factors not included in the a priori model set are identified with a dash (—). Model variables include study area (SA), temporal variation by yr (YR), temporal variation by month (Month), age of individual birds (i.e., juv or ad; Age), gender of individual birds (Gender), forest association (i.e., classification of each study site as oak–hickory or mixed-mesophytic forest association based on canopy tree species composition; Forest), the $\bar{x}$ no. Cooper's hawks and owls observed/hr by season (Raptor), the mean no. of rabbits and squirrels observed/hr by season (Prey), temporal variation by season (Season), and $\bar{x}$ min. monthly temp in winter ($\mathrm{MMNT}_{(\mathrm{win})}$).

annual survival in the Appalachian region ranged from 38% to 46%. Using the known-fates model with covariates, mean annual survival ranged from 44% to 53% across years.

Our estimates of ruffed grouse annual survival in the Appalachian region were slightly higher but within the range of previously reported rates from the central portion 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 ranged from 25% (Small et al. 1991) to 34% (Dorney and Kabat 1960). In Minnesota, annual survival was 11% (Gutierrez et al. 2003). Annual survival in Alberta was 27–30% (Rusch and Keith 1971). Survival ranged from 25% to 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%, autumn survival from 74% to 83%, and winter survival from 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 reported from the central portion of ruffed grouse range. In central Wisconsin, adult and juvenile summer survival was 85% and 65%, respectively; spring survival was 73% and 50%, respectively; autumn survival was 65% and 48%, respectively; and winter survival was 57% and 55%, respectively (Small et al. 1991). Winter survival of ruffed grouse translocated to Tennessee from Michigan and Wisconsin was 45% (White and Dimmick 1978). Winter 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 (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 (Fig. 5). Avian predators were the leading cause of predation, followed by mammalian predators and unidentified predators. We assigned mortality agents based on inspection of carcass remains and signs surrounding the relocated carcass or radiotransmitter, but Bumann and Stauffer (2002) concluded scavenging by mammalian predators altered field evidence of avian predation. Consequently, 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 the primary predators of ruffed grouse, but goshawks are uncommon in the Appalachian region (Bumann and Stauffer 2004). The primary predators in the Appalachians are Cooper's hawk (*A. cooperii*) and owls (Bumann and Stauffer 2004). Avian predation rates in the Appalachian region increased during autumn and spring raptor migrations (Bumann and Stauffer 2004).

Harvest accounted for a smaller portion (12%) of all known mortalities compared to previous studies. Harvest did not appear to increase during the late season (i.e., Jan and Feb, Table 32). Harvest accounted for 13–20% of known mortalities in New York (Bump et al. 1947), 40% and 28% in Wisconsin (DeStefano and Rusch 1986, Small et al. 1991), and 19–48% in Alberta (Fischer and Keith 1974). Harvest (8.6% of known mortalities) was a minor source of grouse mortality in Ohio (Swanson et al. 2003).

Factors influencing survival.—Several factors influenced ruffed grouse survival in the central and southern Appalachian region (Table 36). Further, our results indicated adult annual survival is higher in oak–hickory forests than in mixed-mesophytic 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 ≥55%) and the "high mortality mode" is characterized by annual mortality rates >45% (or annual survival ≤55%). They also noted ruffed grouse exhibit both modes throughout its range. Our estimates suggest grouse exhibit the low mortality mode in oak–hickory forests and high mortality mode in mixed-mesophytic forests.

Bergerud and Gratson (1988) proposed 2 hypotheses to explain the presence of high and low mortality modes. The "predator–cover" hypothesis suggests grouse survival rates will be higher if population(s) of effective predator(s) are reduced or absent. Throughout most ruffed grouse range, the most effective predator is the northern goshawk, but goshawks are uncommon in the central and southern Appalachian regions. During the course of the ACGRP, field personnel reported only 5 sightings of goshawks, each during autumn or spring migration (Bumann and Stauffer 2004). Our estimates of higher adult survival in the Appalachian region and the scarcity of goshawks in the region support the predator–cover hypothesis, but this hypothesis cannot explain the observed differences between oak–hickory and mixed-mesophytic forests. Goshawks are not common in either forest association in the Appalachian region, but other raptors are, including Cooper's hawk and owls, suggesting differential survival between forest associations must be due to $\geq$1 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. Our results provide support that differential reproductive risks may result in differential adult survival. Female grouse in oak–hickory forests had lower nesting rate, nest success, renest rate, clutch size, and chick survival, but had higher adult survival than female grouse in mixed-mesophytic forests.

The influence of age on ruffed grouse survival is unclear. We conducted our survival analyses using multiple time scales (i.e., 5 yr, 1 yr, and 3 months) and subsets of the ACGRP database. In our analysis of survival from April 1997 to 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 our finding. First, age did 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 (i.e., juv and ad) and juveniles surviving >1 year were not reclassified as adults. This classification system limits our ability to investigate more complex age structures. Specifically, if the functional relationship between age and annual survival were actually a quadratic form, fitting a linear model with 2 age classes would indicate age does not influenced survival.

In contrast, our analyses of 1-year data sets (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 of the beta estimate for age overlapped zero indicating age had a weak or nonexisting influence on survival.

We also conducted season-specific analyses (using a monthly time step) and assumed each season (i.e., autumn 1997, autumn 1998, autumn 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 a juvenile in autumn 1998, survived to the next autumn and then graduated to an adult. This bird would have been included in the autumn analysis as 2 individuals, a juvenile in autumn 1998 and an adult in autumn 1999. We found evidence that adult grouse had higher survival in autumn (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 autumn and winter than juveniles, but the difference is small. Second, some individual birds are genetically superior and have greater longevity than others have. 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. 1989*a*). Ideally, researchers would maintain $\geq$30 radiomarked 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 ruffed grouse 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 had a minor influence on ruffed grouse survival and probably operates only during short windows, specifically early autumn (e.g., Sep). We believe the influence of age on survival varies temporally and spatially which would explain the contrasting results in our study and in published literature. We suggest variation in extrinsic factors (e.g., weather conditions, predator composition and abundance) and intrinsic factors (e.g., F condition in spring) more strongly influences juvenile than adult survival and will cause juvenile survival to differ from adult survival in some years and locations. Additionally, measurement error due to sample size and composition influences results and can obscure the true relationship between ruffed grouse age and survival.

The influence of gender on ruffed grouse survival is also debatable. Our analysis of the 5-year data set and annual data sets 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 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 spring than females. We suggest the influence of gender on survival operates during a short period in spring and varies temporally and spatially. During the course of the year, the influence of gender on survival in the Appalachian region is probably minor.

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 was compensatory (regardless of gender or age) at the level of harvest documented. We caution researchers and managers to 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 the ability to conduct controlled, replicated field experiments that can falsify hypotheses (Romesburg 1981). We based our study design on a completely randomized block design with repeated measures, but due to financial, logistical, and political constraints, we faced 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 data were not collected during both 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 assign treatments randomly (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 (VA-3, WV-1, KY-1) with the highest harvest rates during Phase I (1996, 1997, and 1998). We reasoned that if we did not to detect an effect from removing hunting from study areas with the highest harvest rates, a hunting effect likely did not exist at the observed levels of harvest. The most important consequence of this nonrandom 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 1996–1998 and 1998–1999) was 20%. In comparison, mean ruffed grouse harvest rates ranged from 13% to 20% in New York (Bump et al. 1947) and from 29% to 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 Bennett 1963). Importantly, annual harvest rates declined on control areas from 1997 to 2000 and then increased until the end of the study (Fig. 9). 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 (Zwickel 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 autumn population on one study area and compared overwinter survival to an adjacent reference area in 3 consecutive years. Overwinter 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 that harvest mortality is a minor component in ruffed grouse population dynamics (Bump et al. 1947). 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 a density-dependent growth rate, but 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 Alberta, 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 that reduction in natural morality rates could compensate for 41% of the harvest mortality (Fischer and Keith 1974). However, there was no correlation between ratios of population change (Oct–May) and harvest rate, indicating autumn hunting may have been compensatory (Fischer and Keith 1974).

Numerous studies have concluded harvest mortality is compensatory. In western North Carolina, ruffed grouse abundance did not differ before, during, or after the hunting season in small woodlots with 3 levels of prescribed hunting pressure (no hunting, moderate hunting, and unrestricted hunting; Monschein 1974).

Although this study was based on flush counts of unmarked birds, later researchers have drawn similar conclusions. Gullion and Marshall (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 suggested changes in natural mortality could compensate for 30% harvest rate (Jenkins et al. 1963). In Ohio, harvest accounted for 8.6% of mortalities and was compensatory (Swanson et al. 2003). Harvest mortality was compensatory in Michigan (Clark 2000). Harvest of male black grouse (≤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 1979).

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 nonhunted sites, but the results are not conclusive because the populations were not closed. By comparing spring densities between hunted and nonhunted areas, researchers concluded 40% removal of the autumn population of rock ptarmigan (*L. muta*) did not influence spring densities (McGowan 1975). These results suggested harvest mortality was compensatory, but the authors argued immigration to the hunted areas was an important part of the apparent compensatory response. In Colorado, researchers concluded immigration into hunted areas maintained low, but stable densities of white-tailed ptarmigan (*L. leucura*; Braun and Rogers 1971). Immigration supported 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 Bennett 1963). Hunter behavior may explain these findings: for example, most ruffed grouse hunting in Michigan, Maine, and Wisconsin occurs within 402 m of roads (Gullion 1983). It is likely 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 produce immigrants into areas that experience high hunting pressure.

Although we believe regulated sport harvest did not have a direct impact on ruffed grouse survival, there is evidence that disturbance from hunting influenced habitat selection and home range size of ruffed grouse in the Appalachian region (Whitaker et al. 2006, 2008). Ruffed grouse (regardless of gender and age classes) made greater use of clearcuts, roads, and mesic bottomlands and had smaller home ranges in the absence of hunting (Whitaker et al. 2006). These findings suggest hunting pressure may push ruffed grouse out of high and into low quality habitat. We believe recreational disturbance, including hunting, deserves consideration in the development of ruffed grouse hunting regulations and land management plans.

Population Modeling

Our modeling exercise provided widely variable estimates of λ between models and across spatial scales (Table 35). The estimated mean λ from model 1 (0.78) was lower than the observed trend in ruffed grouse abundance in the Appalachian region (−5% change/yr) 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). 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 was due to differences in estimated fecundity (i.e., the no. of chicks that survive to 35 d posthatch/F alive on 1 Apr), which affects the number of chicks entering the autumn population and drives the resulting estimate of λ. Further, we believe the differences in the amount and structure of measurement error and covariance incorporated in models 1 and 2 explains the difference in estimated fecundity.

In model 1, fecundity was the function of multiple reproductive parameters (i.e., nest rate, nest success, renest rate) each of which introduces measurement error resulting in increased variation around the mean estimate of fecundity. The increased variation in the model decreases the mean estimate. 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.

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

Considering the differences (i.e., measurement error, covariance, and variation) between models 1 and 2, we believe model 2 is more accurate and reliable because it is more parsimonious. The estimate of mean λ (at the regional scale) from model 2 is more similar to the estimate derived from the Breeding Bird Survey data (Sauer et al. 2004), the only independent data that provide a useful comparison. These findings provide a level of confidence that the model structure and parameter estimates from model 2 are reflective of ruffed grouse population dynamics in the southern and central Appalachian region. However, the Breeding Bird Survey may underestimate ruffed grouse abundance and change over time due to the low density of ruffed grouse and cryptic behavior. Given these limitations, the Breeding Bird Survey cannot serve to fully validate our model structure or estimates.

Prior to developing the population models, we anticipated λ would be higher in mixed-mesophytic forests than in oak–hickory forests. Instead, our estimates indicated λ was higher in oak–hickory forests than in mixed-mesophytic forests. There are ≥2 possible explanations for the apparent high growth rate in oak–hickory versus mixed-mesophytic forests. First, it is possible the increased adult survival in oak–hickory forests is sufficient to compensate for decreased fecundity and result in higher mean λ. Second, our assumption about the relationship between hard mast production and fecundity was incorrect. Based on our reproductive analysis, we modeled fecundity as a function of mast production the previous autumn in mixed-mesophytic and oak–hickory forests. However, it is possible that due to the presence of high quality, consistently available food resources such as cherry and birch, hard mast production does not influence fecundity in mixed-mesophytic forests as strongly as in oak–hickory forests. If true, we would expect to see less temporal variation in mixed-mesophytic forests and higher mean fecundity rate. It is probable that we underestimated fecundity and λ in mixed-mesophytic forests.

Productivity (i.e., chick survival, model 1, Fig. 10; and fecundity, model 2, Fig. 11) had the strongest influence on ruffed grouse population growth rate in the central Appalachian region (Fig. 11). Both models indicated adult winter and autumn survival (Figs. 10, 11) had relatively moderate influence on λ. Similarly, productivity had the greatest influence on sharp-tailed grouse (*Tympanuchus phasianellus*) population growth rate in Alberta (Manzer 2004). Our results indicate management agencies will be able to increase ruffed grouse abundance most efficiently by focusing management efforts on increasing fecundity, particularly chick survival.

Models are simplified representations of complex systems (Starfield 1997); consequently, managers must interpret model results cautiously. 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. Second, we assumed chick survival from 35 days posthatch to brood break-up (approx. 84 d posthatch) was 100%. The consequence of violating this assumption would be an overestimate of recruitment into the autumn population and possibly λ. That our estimates of λ were similar to estimates from the Breeding Bird Survey suggests our models 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 estimates of fecundity and recruitment and to develop long-term monitoring programs to obtain indices of population size and recruitment. Researchers and managers can use data from long-term indices to develop and test predictive population growth models.

Population Ecology

Species may exhibit ≥ 1 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 in the southern and central Appalachian region north into the central portion of ruffed grouse range exhibit clinal population structure.

Evidence of clinal variation in ruffed grouse populations include changes in morphology, physiology, activity patterns, 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 this study, we captured gray and red phase birds on the PA-1 and RI-1 study areas, whereas we captured only red phase birds on study areas south of PA-1 (P. K. Devers, unpublished data). Ruffed grouse also exhibit gradual changes in physiology. For example, on average, ruffed grouse in the central and southern Appalachians are heavier (Rusch et al. 2000) and have greater percent body fat in early spring than ruffed grouse from the Great Lakes region (C. 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 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). Ruffed grouse exhibit gradual changes in population dynamics across their range. Ruffed grouse in the southern and central Appalachians do not exhibit the 10-year population cycle characteristic of populations in the central portion of the species range. In this study we observed changes in ruffed grouse population dynamics between oak–hickory and mixed-mesophytic forests of the Appalachian Mountains (Table 37).

Table 37. Comparison of ruffed grouse mean population vital rates in oak–hickory and mixed-mesophytic forests in the southern and central Appalachian region, USA, 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).

	Forest association		
Vital rate	Oak–hickory ($\bar{x}$)	Mixed-mesophytic ($\bar{x}$)	Northern hardwood[a] ($\bar{x}$)
Nesting rate (%)	86	100	100[a]
Renesting rate (%)	3.2	45	≥46[b]
Clutch size (no. eggs)	9.4	10.4	≥11.0[c]
Nest success (%)	63	70	≥43[d]
Chick survival (%)	21	39	≈50[e]
Adult annual survival (%)	≈50	≈42	≤37[f]

[a] Holzwart (1990), Balzer (1995), Small et al. (1996).

[b] Rusch and Keith (1971), Balzer (1995), Small et al. (1996), Larson (1998).

[c] Cringan (1970), Rusch and Keith (1971), Maxon (1978).

[d] Rusch and Keith (1971), Maxon (1978), Holzwart (1990), Balzer (1995), Small et al. (1996).

[e] Marshall and Gullion (1965), Rusch and Keith (1971), Beckerton and Middleton (1982).

[f] Dorney and Kabat (1960), Rusch and Keith (1971), Small et al. (1991), Gutierrez et al. (2003).

We suggest 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 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 intraspecific 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. 2004*a*, *b*). 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), prebreeding body condition (Long et al. 2004*b*), and reproduction and recruitment. 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). 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 these conditions in oak–hickory forests favor adult survival over reproduction. This would explain why we observed lower reproductive rates and higher adult survival rates in the Appalachian region compared to the central portion 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 buds of aspen, cherry, and birch. We believe individual grouse in mixed-mesophytic and northern hardwood forests maximize lifetime fitness by favoring reproduction over adult survival.

The relative importance of nutrition on ruffed grouse ecology in the southern and central Appalachians may be a recent event, owing to the loss of American chestnut (*Castanea dentata*) throughout the eastern United States. Hard mast production in the southern Appalachians decreased by 34% after the chestnut blight killed most or all of the mature chestnut trees in the region (Diamond et al. 2000). Further, annual hard mast production was more variable after the blight because oaks and hickories that exhibit high annual variation in hard mast production (Diamond et al. 2000) replaced the American chestnut, a relatively stable hard mast producer. Although few records of ruffed grouse diet exist from the preblight period, Bump and Jones (1947:188) reported, "Chestnuts, in the old days before the blight, were a popular food item in the fall . . . ." The loss of chestnuts may have initiated nutrition as a primary factor influencing ruffed grouse ecology in the southern and central Appalachians.

We note food availability and quality are not the only factors influencing ruffed grouse populations in the central and southern Appalachians, but we believe it may be the current minimum limiting factor. 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), predator communities (Bump et al. 1947, Gullion 1970), and phylogenetic history may contribute to spatial variation in ruffed grouse population ecology and life-history strategies.

Due to their popularity as a gamebird, state management agencies have translocated ruffed grouse throughout much of the United States. Successful translocations in theory could influence population characteristics including morphology, behavior, and dynamics. However, management agencies have not translocated ruffed grouse to or from any of our study areas so we do not believe our results are an artifact of previous management activities.

MANAGEMENT IMPLICATIONS

Ruffed grouse populations in the southern and central Appalachians have lower productivity, but higher survival than populations from in the central portion of ruffed grouse range (Table 37). Our results also indicated ruffed grouse population ecology differs between oak–hickory and mixed-mesophytic forests. Further, our results showed ruffed grouse productivity is influenced by hard mast production in autumn and harvest mortality is compensatory (at current levels).

Elasticity analyses indicate which demographic parameters have the greatest influence (in theory) on λ. 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 by increasing autumn and winter survival. However, we believe it is not biologically or logistically possible to increase autumn and winter survival. First, our estimates of adult seasonal survival were higher than other published rates and we assume they are at or near the maximum survival rate for ruffed grouse. Second, our results indicated present levels of harvest mortality were 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 minimum limiting factor for ruffed grouse population growth in the southern and central Appalachians is productivity. Therefore, 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 interspersion of nest and brood cover among early-successional stands. We also recommend ruffed grouse harvest plans focus on providing high quality hunting opportunities (i.e., low hunting pressure, low vehicle traffic, high flush rates) and not increased harvest rates.

Interspersion of Cover Types

In the Appalachian region, ruffed grouse exhibit daily migrations and seasonal changes in habitat requirements (Schumacher 2002; Whitaker and Stauffer 2003; Jones 2005; Whitaker et al. 2006, 2008). These movements suggests the interspersion of early-successional forest patches (2–16 ha) that provide a diversity of cover types including foraging, escape, and nesting and brood cover is critical to successful habitat management for ruffed grouse in the Appalachian region (Fearer 1999, Whitaker 2003). Interspersion of cover requirements should reduce home range size, movement, predation risk, and energy expenditure, and increase productivity and abundance of ruffed grouse (Jones 2005).

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 increase acorn production. Early-successional forest stands that provide escape cover and food resources can be created using clearcuts with hard mast reserves and shelterwood harvest (Whitaker 2003, Jones 2005, Jones and Harper 2006). Alternatively, harvest units can be planned to intersperse young stands that are adjacent or in close proximity to acorn producing stands. In mixed-mesophytic forests, where alternative food tree species such as birch and cherry are present, we recommend using traditional clearcutting (Whitaker 2003).

Access routes, including logging roads and log landings are important alternative feeding sites for ruffed grouse in oak–hickory forests (Schumacher 2002, Jones 2005, Whitaker et al. 2006). We recommend seeding roads and openings with an initial mixture of clover and small forbs to provide nutritious green forage during winter and sites for broods to glean insects in spring and summer. We also recommend eradicating nonnative perennial cool-season grasses and managing for naturally occurring forbs and grasses arising from the seedbank for optimum brood-rearing habitat (Healy and Nenno 1983, Harper et al. 2001).

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 with precommercial thinning and salvage cuts (Jones 2005). Additionally, small canopy gaps (0.4–2 ha) can be created by girdling trees.

In the southern and central Appalachian region brood cover (to 6 weeks posthatch) is characterized by open mid-age or mature forests stands with a lush herbaceous understory (Haulton 1999, Fettinger 2002). Broods also commonly occur in mesic bottomlands, particularly in oak–hickory forests (Whitaker et al. 2006), presumably due to the higher abundance of herbaceous ground cover and associated arthropod abundance. Broods also used higher elevation (1,300–1,660 m) oak stands on south- and west-facing slopes where the understory was similar to lower elevation mesic sites (Jones 2005). 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 midstory and facilitate growth of herbaceous ground cover (Haulton 1999, Jones 2005).

Hunting

Adult ruffed grouse in the Appalachian region experience high survival rates and current harvest rates (<20%) 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 stands, roads, and mesic bottomlands, in areas open to hunting than in areas closed to hunting (Whitaker et al. 2006, 2008). Thus, we recommend state wildlife agencies in the Appalachian region manage ruffed grouse hunting at current harvest levels and for high quality experiences. We stress that managers should not strive to increase harvest rates beyond those observed in this study because increased harvest mortality may be additive.

To provide high quality hunting opportunities we recommend closing roads in conjunction with habitat management. Hunting pressure, harvest rates, hunter success, and hunting-related disturbance are related to distance from roads or initial starting point (e.g., gate or hunting cabin; Fischer and Keith 1974, Broseth and Pedersen 2000, Gratson and Whitman 2000, Hayes et al. 2002, McCorquodale et al. 2003). In Maine, Michigan, and Wisconsin the majority of ruffed grouse hunting occurs within 402 m of roads (Gullion 1983). We recommend ruffed grouse management units be divided into "refuge" and "recreational" areas. We define refuges as areas receiving habitat management treatments (i.e., timber harvest, prescribed burning, girdling, road seeding) >402 m from any open road (Fig. 12). Refuge areas will provide high quality habitat and 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 stands, access routes, and mesic bottoms; Whitaker 2003). It is possible, although beyond the scope of our data, that refuge areas will produce birds that will disperse across the landscape and may be available to hunters in recreational areas.

Recreational areas are defined as any area <402 m from an open road (Fig. 12). We do not recommend locating all silvicultural prescriptions >402 m from access points. 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 creating small canopy gaps along (open and seeded) roads to provide additional hunting opportunities. This type of configuration will provide high quality habitat across the entire landscape and will minimize disturbance in some portion while providing high quality hunting in the remaining landscape. We cannot make explicit recommendations as to what portion of the landscape or management unit should be maintained as refuge or recreational areas. We encourage implementing our recommendations in an adaptive management framework (Walters and Hilborn 1978) based on local management goals.

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 support road closures (Gratson and Whitman 2000, Little 2001). In areas identified specifically for ruffed grouse management, we encourage closing roads from

Figure 12. Hypothetical 205-ha landscape (adapted 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 m from an open road and are outlined in gray.

the start of the hunting season until the end of the early-brood period (late Jun to mid-Jul). 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-Dec) to the end of the early-brood period. This strategy would 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 require further investigation or management to improve ruffed grouse conservation in the southern and central Appalachian region. First, increasing understanding of the relationship between ruffed grouse productivity and hard mast production is a priority. Second, additional research is needed to determine when harvest mortality becomes additive. We suggest manipulative field studies with specified treatments of 0%, 25%, 50%, and 60% harvest rates. This type of study would provide detailed information on the functional relationship between harvest mortality and survival. Additional research should be conducted to investigate the influence of late-season harvest on ruffed grouse populations. We suggest manipulative field studies with treatments of early-season harvest only (i.e., harvest ends in Dec) and late-season harvest (i.e., harvest continues through Feb). Third, there is a need for population-level genetics research to test the hypothesis that ruffed grouse in the southern and central Appalachian region exhibit clinal population structure. There is a great need for the development of region-wide standardized, annual indices of ruffed grouse population size and autumn age ratios. We recommend conducting periodic (3–5 yr) studies to obtain independent estimates of population size and age ratios to validate annual indices. Independent estimates and indices could be used to develop more reliable, predictive population models that could aid in ruffed grouse management. Finally, we recommend natural resource agencies in the Appalachian region implement a standardized, annual hard mast survey. Managers will be able to use this information to predict changes in ruffed grouse abundance and manage harvest.

SUMMARY

Ruffed grouse in the southern and central Appalachians exhibited lower reproductive rates including nesting rate, renesting rate, clutch size, and nest success than in the central portion of the species range.

Hard mast production strongly influenced ruffed grouse reproductive success in the southern and central Appalachian region.

In the southern and central Appalachians ruffed grouse reproductive rates, including nesting rate (86% vs. 100%), renesting rate (3.2% vs. 45%), clutch size (9.4 eggs vs. 10.4 eggs), and nest success (63% vs. 70%) were lower in oak–hickory than mixed-mesophytic forests.

Ruffed grouse chick survival to 35 days posthatch was extremely low in oak–hickory (21%) and mixed-mesophytic (39%) forests.

Adult annual survival of ruffed grouse in the southern and central Appalachians was higher than in the central portion of the species range.

Adult ruffed grouse annual survival was higher in oak–hickory (50%) than in mixed-mesophytic (42%) forests.

In the southern and central Appalachian region, harvest mortality of 20% was compensatory.

Chick survival had the greatest influence on ruffed grouse finite population growth in the southern and central Appalachian region.

Managers should focus efforts on the juxtaposition of forest cover types and age classes to provide foraging, loafing, and security cover.

Harvest management should focus on providing high quality hunting opportunities (i.e., low hunter pressure, increased flush rates) and not on increasing harvest rates.

Natural resource agencies should implement a standardized, regional survey of annual hard mast production to aid in predicting changes in abundance and managing harvest.

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Ruffed grouse chick in West Virginia, USA. Photo by Tom Allen, West Virginia Department of Natural Resources.