

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/261974023>

Fall–Winter Survival of Ruffed Grouse in New York State

Article in *Northeastern Naturalist* · December 2011

DOI: 10.2307/41429229

CITATIONS

7

READS

204

4 authors, including:



[Megan M Skrip](#)

North Carolina State University

9 PUBLICATIONS 101 CITATIONS

SEE PROFILE

Fall–Winter Survival of Ruffed Grouse in New York State

Megan M. Skrip^{1,2,*}, William F. Porter^{1,3}, Bryan L. Swift⁴,
and Michael V. Schiavone⁴

Abstract - In New York, *Bonasa umbellus* (Ruffed Grouse) abundance has declined since the 1960s, presumably due to forest maturation. Wildlife managers expressed concern that hunting may contribute to the population decline as habitat quality decreases. We monitored fall–winter survival of 169 radio-marked Ruffed Grouse at 2 study areas in New York differing in forest age and composition. Fewer than 11% of radio-marked birds were harvested, and seasonal survival was similar at the 2 study areas in both study years (0.38 and 0.51, 2007–2008; 0.48 and 0.48, 2008–2009). Predation, particularly by raptors, was the largest source of mortality, but locations of predation events were not associated with forest age or configuration within 300 m. We found no evidence to support a reduction in harvest limits, although our harvest estimates may have been biased low.

Introduction

Sustainable wildlife management depends on reexamining existing management policies in light of changing habitat conditions. As habitat quality for *Bonasa umbellus* L. (Ruffed Grouse) declines throughout the Northeast due to forest maturation (DeGraaf and Yamasaki 2003, Dessecker and McAuley 2001), wildlife managers express concern that harvest regulations may require revision. Ruffed Grouse have long been popular quarry for sportsmen in North America (Edminster 1954), and the impact of harvest on populations has been the subject of many studies (e.g., Clark 2000, DeStefano and Rusch 1986, Devers et al. 2007, Dorney and Kabat 1960, Edminster 1937, Fischer and Keith 1974, Palmer and Bennett 1963, Small et al. 1991). However, the combined contribution of harvest and declining habitat quality to mortality, particularly in declining Ruffed Grouse populations, has not been addressed outside of the Appalachians. Ruffed Grouse could be at greater risk of harvest in areas with increasingly inadequate cover and, thus, it is important to assess the effect of harvest on declining populations as habitat conditions change at broad scales.

Continent-wide, Ruffed Grouse populations have declined 54% since the mid-20th century as high-quality early-successional habitat has disappeared (National Audubon Society, Inc. 2008). In New York State alone, Ruffed Grouse have declined 5% per year 1966–2007, and as much as 16% per year since 1980 (Post 2008, Sauer et al. 2008), as forests regenerating from abandoned farmlands

¹Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210. ²Current address - Department of Natural Resources Science, 105 Coastal Institute in Kingston, University of Rhode Island, 1 Greenhouse Road, Kingston, RI 02881. ³Current address - Department of Fisheries and Wildlife, 13 Natural Resources Building, Michigan State University, East Lansing, MI 48824. ⁴New York State Department of Environmental Conservation, 625 Broadway, Albany, NY 12233. *Corresponding author - megan_skrip@my.uri.edu.

have matured. Despite changes in population size, Ruffed Grouse remain the second most popular game bird in New York (after *Meleagris gallopavo* L. [Wild Turkey]; New York State Department of Environmental Conservation, Albany, NY, unpubl. data). The last assessment of Ruffed Grouse survival and harvest mortality in New York was performed over a half-century ago (i.e., Bump et al. 1947). Our investigation responded to concerns that harvest may contribute to the decline of Ruffed Grouse in the state, as New York has one of the longest hunting seasons in the Northeast.

Young, early-successional forest with high stem densities is ideal habitat for Ruffed Grouse (Thompson and Dessecker 1997). We proposed that landscapes consisting of large patches of mature forest may necessitate larger home range sizes and consequently favor human and predator encounters, contributing to higher mortality. Conversely, high availability of early-successional habitat may improve survival by providing better cover and food resources, thereby decreasing energy demands, activity times, and predator encounters (Endrulat et al. 2005, Fearer and Stauffer 2004, Hewitt and Kirkpatrick 1997, Whitaker et al. 2007, Yoder et al. 2004). Within home ranges, dense vertical cover of saplings and shrubs is essential for shielding Ruffed Grouse from predators (Dessecker and McAuley 2001, Thompson and Dessecker 1997), including hunters.

We examined Ruffed Grouse survival through 2 hunting seasons in 2 areas of New York State with different forest age and composition, and we assessed the contribution of harvest to overwinter mortality. We predicted that fall–winter survival would be higher, and harvest rate lower, in the study area dominated by young, early successional forest, i.e., that Ruffed Grouse mortality is lower in higher-quality habitat. We expected that mortality locations of Ruffed Grouse would occur more frequently in older forest than was available at random. If our predictions were correct, modifications to harvest limits or forest management in some areas of the state might be considered by management agencies.

Field Site Description

The two field sites chosen for this 2007–2008 and 2008–2009 investigation were 1943 ha of the Fort Drum Military Installation in Jefferson County, NY, and the 1859-ha Partridge Run Wildlife Management Area in Albany County, NY. Fort Drum (44°3'N, 75°33'W) is <80 km east of Lake Ontario in New York's Western Adirondack Transition zone adjacent the Eastern Ontario plain (NYSDEC Habitat Inventory Unit 1990) in the Laurentian Mixed Forest Province (Bailey 1995). Partridge Run (42°34'N, 74°11'W) is approximately 32 km west-southwest of Albany in the Helderberg Highlands region of New York's Appalachian Plateau (NYSDEC Habitat Inventory Unit 1990), with vegetation typical of the Eastern Broadleaf Forest Province (Bailey 1995). Ruffed Grouse hunting seasons opened on 20 September at Fort Drum and 1 October at Partridge Run and closed at both areas on the last day in February both study years. Both areas were popular sites for small- and big-game hunting (C. Dobony, Fort Drum Fish and Wildlife Management Program, Fort Drum, NY, and B. Swift, New York State Department of Environmental Conservation, Albany, NY, pers. comm.) and represented areas with some of the highest grouse hunting pressure in the state.

Fort Drum and Partridge Run varied in tree species composition and stand size class distribution. Fort Drum was dominated by second-growth forests regenerated from farmland abandoned in the 1940s (Dobony and Rainbolt 2008). Forest there was predominantly early and mid-successional (*Populus grandidentata* Michx. [Bigtooth Aspen], *Populus tremuloides* Michx. [Quaking Aspen], *Betula* spp. [birch], *Prunus* spp. [cherry], *Acer* spp. [maple], and *Pinus* spp. [pine]), with some mature plantations of *Pinus sylvestris* L. (Scots Pine) and *P. resinosa* Soland. (Red Pine). At Partridge Run, forests regenerated from marginal agricultural lands abandoned in the 1930s in the Helderberg Highlands (Moser et al. 2001). Our study area there consisted mainly of mature mixed hardwoods (maple, birch, cherry, *Fraxinus* spp. [ash], *Quercus* spp. [oak], and *Fagus grandifolia* Ehrh. [American Beech]) and some mature conifer plantations (including pine and *Picea abies* L. [Norway spruce]), with scattered abandoned *Malus* spp. (apple) orchards.

Fort Drum had nearly twice as much seedling-sapling forest (2–12 cm diameter at breast height [DBH]) than Partridge Run (14% of forest at Fort Drum vs. 7.2% at Partridge Run; C. Dobony, unpubl. data; Moser et al. 2001). The majority of forest at each area was pole timber (13–28 cm DBH; 58% at Fort Drum, and 82.3% at Partridge Run), with a saw timber (>28 cm DBH) component (28% of Fort Drum forest, and 10.4% of Partridge Run forest) (C. Dobony, unpubl. data; Moser et al. 2001).

Methods

Field techniques

We captured Ruffed Grouse at Fort Drum and Partridge Run in autumn 2007 and 2008 using modified lily-pad traps (Bucks et al. 1985, Gullion 1965, Hunyadi 1984). At Fort Drum, birds were captured 11 September–5 October 2007 and 4 September–6 November 2008. At Partridge Run, birds were captured 6–28 September 2007 and 2–18 September 2008. We checked traps twice a day, once in the morning and once in late afternoon to evening. We fit Ruffed Grouse with an anodized aluminum butt-end band and a 5.6-g (2007 only) or 10.7-g (2007 and 2008) necklace-style VHF radio-transmitter (Advanced Telemetry Systems, Isanti, MN) with either an 8-hr (2007 only) or 4-hr (2008 only) mortality switch (Devers et al. 2007). Bands and radio-transmitters were labeled with toll-free telephone numbers to encourage hunters to report harvested birds. All capture and handling procedures were conducted under the approval of the Institutional Animal Care and Use Committee of the State University of New York College of Environmental Science and Forestry (IACUC Protocol No. 2007-7).

We determined the sex of captured Ruffed Grouse by counting the number of spots on rump feathers and observing the continuity of the sub-terminal tail band (Bump et al. 1947, Roussel and Ouellet 1975, Servello and Kirkpatrick 1986). We differentiated adult (after-hatching-year) and juvenile (hatching-year) birds by the curvature of the ninth and tenth primary feathers and the presence or absence of primary feather sheathing (Dorney and Kabat 1960). We knew of no problems with these criteria in New York State.

We monitored the status of radio-marked Ruffed Grouse via radio-telemetry 2–3 times a week from the time of capture through the end of the hunting season (29 February 2008 and 28 February 2009). Upon detection of a mortality signal, we retrieved the transmitter and remains, recorded the location with a GPS unit, and determined cause of death via standard field sign (Bumann 2002). We classified mortality sources as harvest, avian predation, mammalian predation, unknown predation, other, or unknown. Harvests were reported by hunters or determined via field sign. We assigned the date of mortality to midpoint between the last live signal detected and the first mortality signal (Devers et al. 2007). We right-censored all birds with which we lost contact (dropped collar, transmitter failure, or signal loss) or which survived the analysis interval (Pollack et al. 1989a, b). For censored birds with unknown fates, we assigned the date of censor to the day after the last date of detection (Devers et al. 2007). For all birds still alive at the end of the hunting season, we assigned the censor date as the last day of the respective hunting season. Two birds lost from the 2007–2008 season due to battery failure were re-captured autumn 2008 and re-admitted to the study at that time with new functioning transmitters. Because their fates were known, these two birds were censored from the 2007–2008 study interval at the end of the hunting season rather than upon transmitter failure. We excluded from analysis any Ruffed Grouse that died less than 1 week post-capture, to control for capture-related transmitter effects (Clark 2000, Devers et al. 2007). In total, 169 Ruffed Grouse were included in survival analyses.

Survival analyses

We estimated fall–winter survival through the hunting season for study areas, sexes, and age classes via the Kaplan-Meier product-limit estimator in SAS (Kaplan and Meier 1958, SAS Institute Inc. 1999), using code from White and Garrott (1990) to allow for staggered entry (Pollack et al. 1989a, b; Roberts 1993). We compared survival distributions using the log-rank test. We used a 2-tailed Z statistic to test for differences in survival rate at the end of the hunting season, with a significance level of $\alpha = 0.05$ (Pollack et al. 1989a, Roberts 1993). We compared survival distributions within study areas between years after Migoya and Baldassarre (1995). We used 2 September (the earliest capture date) as an interval start point (White and Garrott 1990) to compare year-to-year and study-site variation. For comparisons between sexes and age groups, individuals were pooled across study areas.

We performed a stratified, cause-specific risk analysis using Cox regression in SAS (PROC PHREG) with data duplication (Heisey and Patterson 2006, Lunn and McNeil 1995). Lunn and McNeil (1995:527–8) describe an approach to fitting a stratified proportional hazards model in which the stratification variable is risk type (δ), allowing the baseline hazard to vary by risk type. The covariates are coded as the pairs δx_1 , δx_2 and $(1 - \delta)x_1$, $(1 - \delta)x_2$, replacing main effects and interactions with fully specified interactions. This model yields coefficients as if fitting a separate proportional hazard model for each risk type. We fit a full model with effects of age (0 = adult, 1 = juvenile), sex (0 = male,

1 = female), and study area (0 = Fort Drum, 1 = Partridge Run) on the risk of harvest vs. non-harvest mortality (i.e., on harvest hazard vs. non-harvest hazard). Non-harvest mortality consisted mainly of predation, with a small component of non-predation and unknown cause. We pooled all data from both 2007–2008 and 2008–2009 seasons and used a significance level of $\alpha = 0.05$.

Landscape analyses

To compare overall landscape composition and arrangement between study areas, we used location information to estimate the total area used by study birds. For each study area, we overlaid recovery and trap locations from the 2008–2009 season on a 2001 National Land Cover Data (NLCD) raster in ArcMap (ESRI 2006) and determined the straight-line distance (m) between trap site and recovery site for each bird captured (Thomas and Taylor 2006). Recovery location data from the 2007–2008 season were incomplete. We found 1.5 km to be the average distance from trap to recovery (range 79 m to 7.7 km) and, therefore, generated 1.5-km-radius buffers around each recovery and trap coordinate, dissolving those buffers at each site to form study area boundaries. The dissolve yielded a Fort Drum analysis area of 6133 ha and Partridge Run area of 5728 ha. We used FRAGSTATS (McGarigal et al. 2002) to calculate the following metrics in each area: percentage of each land cover class (PLAND), patch density (PD), edge density (ED), contrast-weighted edge density (CWED), mean patch shape index (SHAPE), interspersion and juxtaposition index (IJI), and patch richness (i.e., number of different landscape classes present; PR).

To compare landscape characteristics between mortality locations and random locations within study areas, we used ArcMap to cast 50 random points within each study area boundary and compared those points to predation locations of grouse during the 2008–2009 field season (Fort Drum, $n = 18$; Partridge Run, $n = 15$). We buffered each predation and random point by a 300-m-radius (28.44-ha) circle to approximate the average home range size of a Ruffed Grouse around each location (Fearer 1999). We used FragStatsBatch (Mitchell 2005) to calculate metrics within each buffer (Brown and Litvaitis 1995, Fearer 1999, Thogmartin and Schaeffer 2000) and used all of the metrics evaluated in the study area comparison except for percentage of each land-cover class. To avoid multicollinearity among PLAND variables, we included only percent shrub (PLAND for shrub), percent forest (pooled PLAND for deciduous, mixed, and evergreen forest and woody wetlands), proportion evergreen (PLAND for evergreen divided by pooled forest PLAND), and proportion deciduous. We performed a correlation analysis using PROC CORR in SAS to compare landscape metrics and eliminated the less biologically meaningful variable of pairs with $\rho \geq 0.7$ to further avoid multicollinearity. We used PROC LOGISTIC in SAS (stepwise selection, $\alpha = 0.05$) to develop models differentiating predation locations and random locations (Henner et al. 2004, Kunkel and Pletscher 2000, Thogmartin and Schaeffer 2000). We used area under the curve values from receiver operating characteristic (ROC) curves to evaluate model discriminatory performance (Fielding and Bell 1997, Pearce and Ferrier 2000).

At Fort Drum, an additional forest inventory dataset managed by installation personnel allowed comparison of forest stand size class between predation and random points (C. Dobony, unpubl. data). For each mortality location ($n = 16$) and random location ($n = 34$) for which this information was available, we used the Fort Drum coverage to determine size class (seedling-sapling, pole, saw timber) of the patch containing each point. We used Fisher's exact test to test whether size-class frequency differed between predation and random locations (McDonald 2009). We expected that a greater frequency of predation locations would be in saw timber patches than in random locations, and a lower frequency would be in seedling-sapling patches than in random locations.

Results

Mortality sources and their temporal distribution

Over both study areas and years, 48–58% of 37–50 radio-marked Ruffed Grouse were confirmed mortalities through the hunting season, due to several mortality sources. Predation, particularly by raptors, was the largest source of mortality (Table 1). At each study area, 39% (Partridge Run) and 55% (Fort Drum) of all mortalities were confirmed predation events in 2007–2008, although these values are likely biased low because unknown determinations may have been predation. In 2007–2008, interference by scavengers and weather conditions complicated mortality diagnoses, contributing to an elevated number of unknowns. In 2008–2009, 91% of mortalities at Fort Drum and 62% at Partridge Run were due to predation, . Hunting represented 0–22% of all mortalities across study areas and years and was the mortality source of 0–11% of all captured birds. At both study areas, several birds each year lost contact and were right-censored: 3 in 2007–2008 and 4 in 2008–2009 at Partridge Run, and 5 in 2007–2008 and 1 in 2008–2009 at Fort Drum.

Table 1. Mortality sources of radio-marked Ruffed Grouse at Fort Drum and Partridge Run, NY, 2007–2008 and 2008–2009. In 2007–2008, some “unknown” determinations were likely predation but not recorded as such; in 2008–2009, “unknown” indicates inaccessibility of the remains.

	Fort Drum		Partridge Run	
	2007–2008	2008–2009	2007–2008	2008–2009
No. of birds in study	38	44	37	50
Total confirmed mortalities	22	21	18	26
Total harvest	3	0	4	3
Total non-harvest	19	21	14	23
Raptor	6	13	2	10
Mammal	2	5	1	2
Unknown predator	4	1	4	4
Unknown	7	1	7	3
Other ^A		1		4
Lost transmitter or signal	5	1	3	4
Survived hunting season	11	22	16	20

^AOne Ruffed Grouse was sealed in a snow roost by an ice storm at Fort Drum. At Partridge Run, 3 were killed by vehicles, and 1 whole carcass was found without evidence of predation.

Harvest mortality was low and similar between study areas in 2007–2008, but displayed different temporal patterns (Fig. 1). Three birds were harvested at Fort Drum and 4 at Partridge Run in 2007. We documented no harvest of radio-marked Ruffed Grouse at Fort Drum and 3 at Partridge Run during the 2008–2009 hunting season. At Fort Drum in 2007–2008 and Partridge Run in 2008–2009, monthly mortality was highest in October and late winter; in 2007–2008 at Partridge Run and 2008–2009 at Fort Drum, mortality peaked in November (Fig. 1).

At Fort Drum, 1 adult female (of 6 marked), 1 adult male (of 7 marked), and 1 juvenile female (of 14 marked) were harvested in the 2007–2008 season. At Partridge Run, across both seasons, 2 adult females (of 10), 2 adult males (of 19), and 3 juvenile females (of 26) were harvested. In total, 14% of 42 adults and 4% of 93 juveniles captured were harvested; 13% of 56 females and 4% of 76 males were harvested. No radio-marked juvenile males (of 53 total) were harvested at either site, although 29 were mortalities.

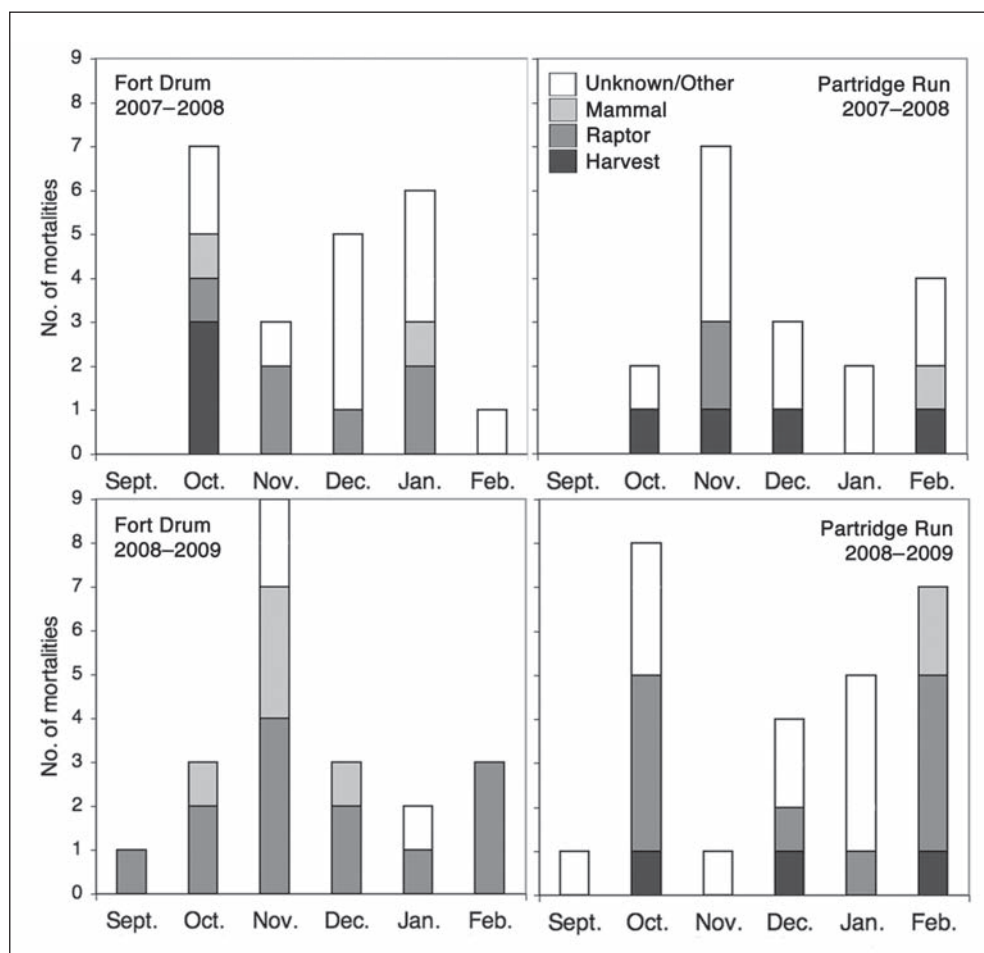


Figure 1. Monthly mortality of radio-marked Ruffed Grouse by source, Fort Drum and Partridge Run, NY, 2007–2008 and 2008–2009.

Survival analysis using the Kaplan-Meier estimator

Survival curves through the hunting season did not differ between Partridge Run and Fort Drum (Figs. 2, 3) for both 2007–2008 (log-rank, $P = 0.99$) and 2008–2009 (log-rank, $P = 0.09$). Male and female survival curves (data pooled across study areas) did not differ in the 2007–2008 season (log-rank, $P = 0.45$), but did in the 2008–2009 season (log-rank, $P = 0.01$). Survival curves differed between adults and juveniles (data pooled across study areas) during both 2007–2008 (log-rank, $P < 0.01$) and 2008–2009 seasons (log-rank, $P < 0.01$). Seasonal survival curves did not differ at Fort Drum between 2007–2008 and 2008–2009 (log-rank, $P = 0.65$), but did so at Partridge Run (log-rank, $P = 0.01$). Unlike survival curves, final survival probabilities at end of hunting seasons did not differ between any comparison classes (Z -test, $P > 0.05$; Table 2).

Competing risks analysis using the Cox model

The harvest hazard of females in our study was 3.62 times the male harvest hazard, and the harvest hazard of juveniles was 25% of the adult harvest hazard

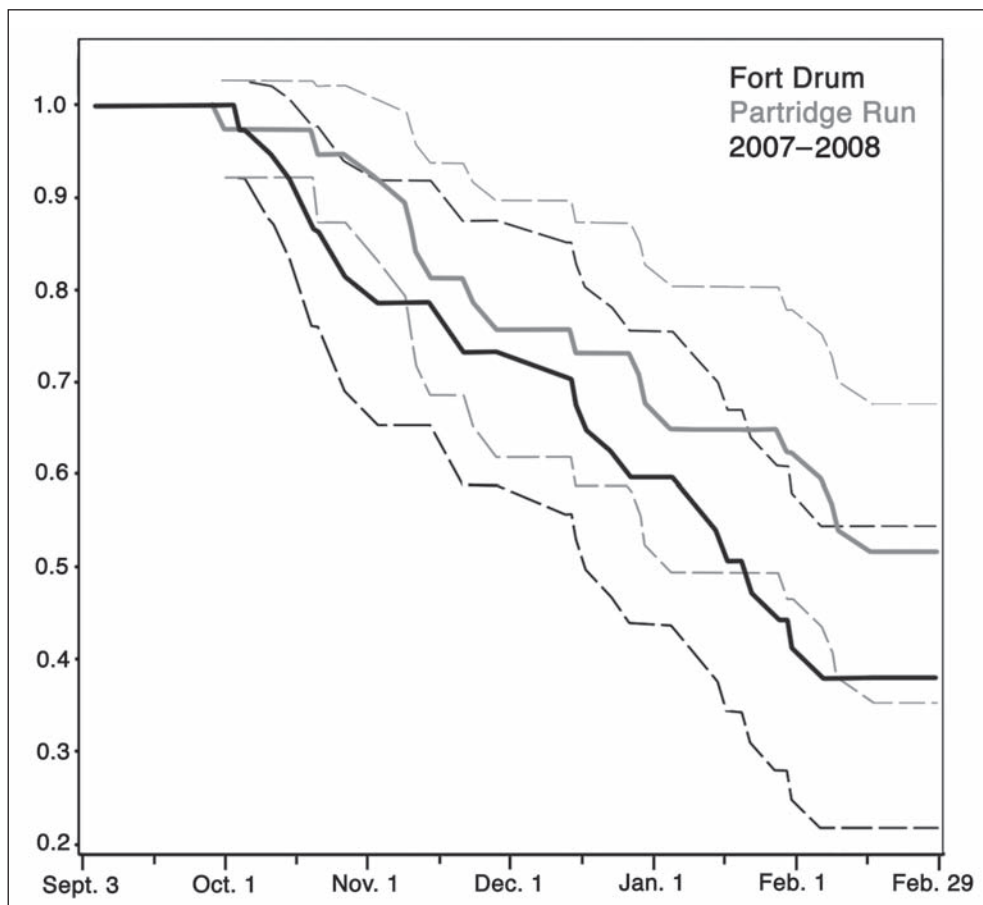


Figure 2. Kaplan-Meier survival probability distributions (solid lines) and point estimate 95% confidence intervals (dashed lines) for Fort Drum (black) and Partridge Run (gray), NY, 2007–2008 (log-rank test, $P = 0.99$).

(Table 3). The harvest hazard of Partridge Run birds did not differ from that of Fort Drum birds (Table 3). None of the demographic variables were significant predictors of predation risk ($P > 0.05$; Table 3).

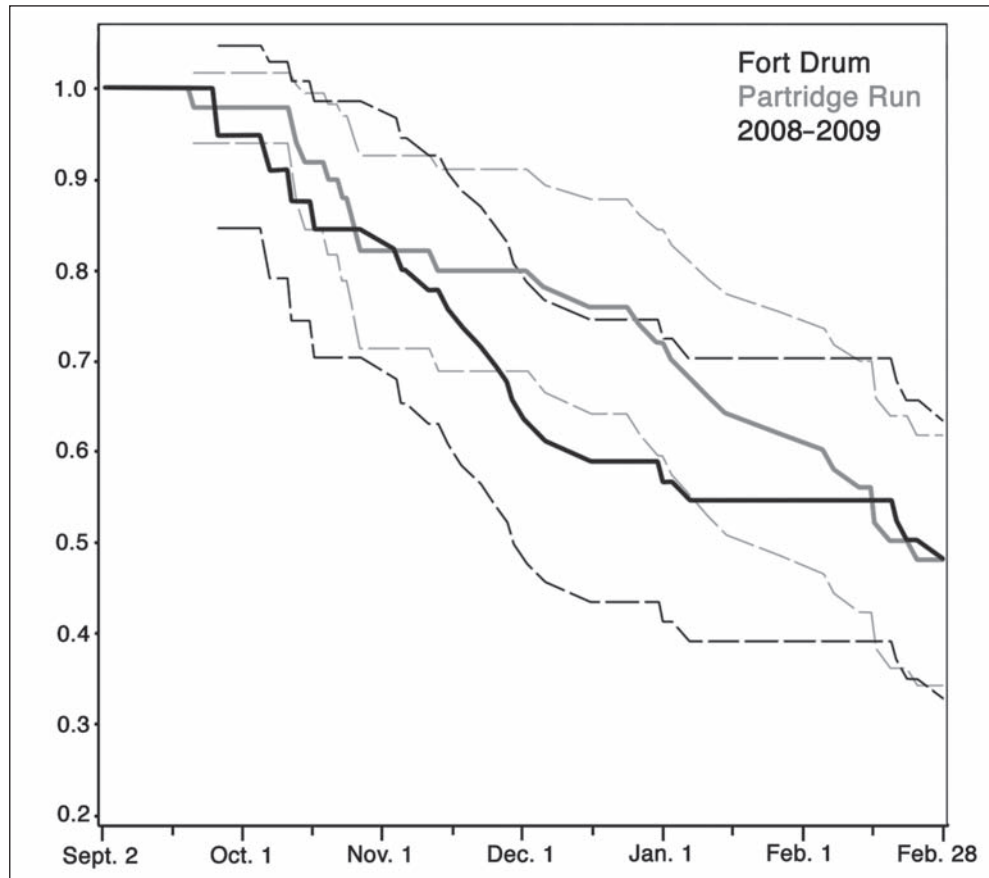


Figure 3. Kaplan-Meier survival probability distributions (solid lines) and point estimate 95% confidence intervals (dashed lines) for Fort Drum (black) and Partridge Run (gray), NY, 2008–2009 (log-rank test, $P = 0.09$).

Table 2. Kaplan-Meier final survival probabilities (S) at end of February, and 95% upper and lower confidence limits, for Ruffed Grouse at Fort Drum and Partridge Run, NY, September–February 2007–2008 and 2008–2009. Males and females, and adults and juveniles, were pooled across study areas.

	2007–2008				2008–2009			
	<i>n</i>	LCL	S	UCL	<i>n</i>	LCL	S	UCL
Fort Drum	38	0.22	0.38	0.54	44	0.33	0.48	0.63
Partridge Run	37	0.35	0.51	0.67	50	0.34	0.48	0.62
Males	35	0.25	0.41	0.58	54	0.27	0.40	0.54
Females	39	0.34	0.50	0.65	37	0.41	0.57	0.72
Adults	24	0.16	0.36	0.56	29	0.26	0.44	0.62
Juveniles	50	0.35	0.49	0.63	61	0.39	0.51	0.63

Landscape analyses

Despite differences in local forest composition and structure between areas, Fort Drum and Partridge Run exhibited similar overall landscape-scale configuration. No variables were significant predictors of mortality location versus random location at either Fort Drum or Partridge Run (models not shown). When study areas were pooled, the final model indicated that predation locations had more forest and greater patch richness than random locations (Table 4). The classification accuracy of the model was low (area under the ROC curve = 0.690), and it was more effective at predicting random locations than predation locations. The true probability that a location was a predation site was 33%, but at a probability level of 0.33, only 42% of predation locations and 82% of random locations were predicted correctly by the model.

Analysis of the Fort Drum forest inventory dataset revealed no difference in tree size-class frequency between mortality and random locations. While a greater proportion of random (vs. mortality) points occurred in sapling patches, and a greater proportion of mortality (vs. random) points occurred in sawtimber patches, this difference was not statistically meaningful (Fisher's exact test, $P = 0.51$).

Discussion

Our objective was to compare the contribution of harvest to Ruffed Grouse mortality during the hunting season in different forest types in New York State. We expected harvest to be lower and survival higher in the study area with more

Table 3. Parameter estimates from a competing-risks model assessing the hazard of harvest versus non-harvest death of Ruffed Grouse based on study area, sex, and age, New York, 2007–2009.

Risk type	Variable	DF	Parameter estimate	Std. error	Chi-square	<i>P</i>	Hazard ratio
Harvest	Study area	1	0.54	0.51	1.10	0.29	1.709
	Sex	1	1.29	0.54	5.60	0.02	3.619
	Age	1	-1.38	0.50	7.50	<0.01	0.252
Non-harvest	Study area	1	-0.32	0.20	2.71	0.10	0.724
	Sex	1	-0.39	0.20	3.76	0.05	0.676
	Age	1	0.11	0.21	0.27	0.60	1.116

Table 4. Parameter estimates (estimated value of regression coefficients) from a stepwise logistic regression model comparing random and predation locations of radio-marked Ruffed Grouse with study areas pooled, New York, 2007–2009.

Parameter	DF	Parameter estimate	Std. error	Wald chi-square	<i>P</i>
Intercept	1	-7.85	2.76	8.11	<0.01
Percent forest	1	0.04	0.02	4.24	0.04
Patch richness	1	0.51	0.19	7.40	<0.01

early-successional forest. Despite differences in seral stage and tree size distribution at Partridge Run and Fort Drum, overwinter survival of Ruffed Grouse did not differ between study areas. Harvest levels were lower than expected, and predation events were not more likely to occur in forest stands of a particular age or landscape configuration than stands at random locations.

Overall harvest and survival rates we observed were comparable to those from decades ago in New York (Bump et al. 1947) and from cyclical grouse populations elsewhere (Davies and Bergerud 1988, Edminster 1954, Rusch and Keith 1971). If harvest rates are similar elsewhere in the state, the level of take we observed suggests that hunting is likely not the driver of grouse population decline in New York (Ellison 1991). Other studies have found that the high background mortality rate of grouse can allow for compensatory survival even at higher rates of harvest (Ellison 1991), although additive harvest mortality was documented in Wisconsin when harvest accounted for 28% of total mortality during hunting seasons (Small et al. 1991). These authors suggest that a regional grouse population may decline when high hunting mortality combines with low immigration caused by landscape fragmentation (Small et al. 1991).

The last empirical assessment of Ruffed Grouse harvest rate in New York was performed by Bump et al. (1947) in the 1930s. These authors concluded that 17% of New York's autumn Ruffed Grouse population was harvested each year (including crippling losses) and that this was not detrimental to the overall population based on continued abundance of breeding stock (Bump et al. 1947:379). Bump et al. (1947:538) further suggest that harvesting up to 20% of the preseason population is not completely additive, citing a three-year study in which harvest losses were greater than overall differences in grouse mortality between a hunted and unhunted area. Seasonal survival ranged from 34% to 61% across areas and years (Bump et al. 1947:538), encompassing the range of survival estimates from our study. At our study areas, we found that $\leq 11\%$ of radio-marked Ruffed Grouse were harvested per year, and that seasonal survival rates were similar in both areas and years despite variability in harvest.

The potential exists, however, that some of the harvest rates found in our study were biased low. At Fort Drum in 2008–2009, no radio-marked Ruffed Grouse were taken by hunters, but poor capture success resulted in a small sample size early in the hunting season, when most hunting activity likely occurred. Across study areas and years, 4 radio signals were lost for unknown reasons and could represent unreported harvest or emigration from the study area or technical failure.

The current hunting season in New York (5–5.5 months) is longer than that during Bump et al.'s (1947) investigation (3 weeks to 1.5 months), and bag limits (4 Ruffed Grouse/day, no season limit) are greater than in the 1930s (3/day, maximum 15/season). Nevertheless, our harvest rates fell within the range of rates estimated 8 decades ago (9.7–15.6% from check stations and 4–28% from recorded harvest per county; Bump et al. 1947:373–375). Across the state, the current average number of Ruffed Grouse harvested per hunter per season (2.8; estimated over 5 years of Cooperator Ruffed Grouse Hunting Log data, New York State Department of Environmental Conservation, Albany, NY, unpubl. data) is

similar to the average estimate over 15 years of data in the 1920s and 1930s (2.9; Bump et al. 1947:372).

Harvest rates in New York appear to be generally at the low end of those reported elsewhere: 5–40% in Wisconsin (Dorney and Kabat 1960), 9% in Alberta, Canada (Rusch and Keith 1971), and 10–30% in Michigan (Clark 2000, Palmer and Bennett 1963). The contribution of harvest to overall mortality at our study areas (0–22% of known deaths) was within the range of estimates from other contemporary studies of radio-marked Ruffed Grouse: 12–35% in Michigan (Clark 2000) and 12% in the Appalachian Cooperative Grouse Research Project (Devers et al. 2007). The final fall–winter survival probabilities we observed (0.38–200.51) are also comparable to those estimated during banding studies of grouse populations elsewhere (Davies and Bergerud 1988, Edminster 1954, Rusch and Keith 1971).

Results of the competing risks analysis suggested that adults and females in our study areas were at greater risk of harvest than juveniles and males. These results are inconsistent with most reports in the literature (e.g., see Clark 2000, Dorney and Kabat 1960, and Small et al. 1991). The low harvest we observed and the timing of trapping at Fort Drum may have resulted in a spurious trend. At Partridge Run, all radio-marked birds were captured before the hunting season, but at Fort Drum, low capture success in 2008 necessitated trapping through October. Birds radio-marked in October were possibly less vulnerable to harvest (or mortality) than birds that went uncaptured and died earlier in the season. Most of these late-season captured birds were juveniles, and more juveniles in the overall sample were males, so results of our analyses may reflect a sampling bias. Consequently, our finding that adults and females were most vulnerable to harvest is open to question.

Our landscape analyses indicated that predation events at Fort Drum and Partridge Run occurred in sites with more forest and greater patch richness than random sites; i.e., Ruffed Grouse were killed in areas more diverse (in terms of number of patch types present) and more forested than random areas. These attributes, however, are typically noted in general as preferred by Ruffed Grouse for inclusion in home ranges (e.g., Fearer and Stauffer 2004). A comparison between live-grouse locations and mortality locations would clarify our findings. At Fort Drum, where recent forest surveys allowed us to examine the vicinity of mortality events on a finer scale, we found no evidence that predation events occurred more often in large-diameter stands than would be expected at random.

Consequences for management

The results of this observational study suggest that, if representative of New York State, overwinter mortality rates of Ruffed Grouse have not changed considerably over 60 years of forest succession. More replication across a gradient of habitat quality is required to quantify the relationship between seasonal survival and forest age and condition. Yet, despite some potential bias in sampling, our evidence suggests that harvest likely does not drive overwinter survival, and that tightening hunting regulations would not curb further population decline. As in

the early decades of Ruffed Grouse research in New York, harvest mortality in our study was not a dominant factor in estimated Ruffed Grouse fall–winter mortality. We, therefore, recommend focusing further investigation towards other factors that may limit grouse abundance, e.g., production. Early-successional habitat may be most important for production, nest success, and brood survival. Devers et al. (2007) demonstrated that spring production drives population growth rates more than overwinter mortality for Ruffed Grouse in the Appalachians. We expect the case is true for New York Ruffed Grouse as well.

Acknowledgments

Financial support for this study was provided by the New York State Department of Environmental Conservation (NYSDEC), including funding from the Federal Aid in Wildlife Restoration Grant WE-173-G. Field support, study-site access, and guidance for planning and conducting this work were provided by numerous NYSDEC and Department of Defense-Fort Drum Military Installation personnel, ESF employees, and volunteers. J. Frair, L. Zhang, D. Keppie, and two anonymous reviewers provided helpful comments on earlier versions of the manuscript.

Literature Cited

- Backs, S.E., P.D. Major, C.H. Eisfelder, and J.S. Thompson. 1985. Techniques for trapping and restocking Ruffed Grouse in Indiana. Indiana Department of Natural Resources. Indianapolis, IN. 13 pp.
- Bailey, R.G. 1995. Description of the ecoregions of the United States. Available online at <http://www.fs.fed.us/land/ecosysmgmt/index.html>. Accessed 1 October 2009.
- Brown, A.L., and J.A. Litvaitis. 1995. Habitat features associated with predation of New England Cottontails: What scale is appropriate? *Canadian Journal of Zoology* 73:1005–1011.
- Bumann, G.B. 2002. Factors influencing predation on Ruffed Grouse in the Appalachians. M.Sc. Thesis. Virginia Polytechnic Institute and State University, Blacksburg, VA. 140 pp.
- Bump, G., R.W. Darrow, F.C. Edminster, and W.F. Crissey. 1947. *The Ruffed Grouse: Life History, Propagation, Management*. New York State Conservation Department, Albany, NY. 915 pp.
- Clark, M.E. 2000. Survival, fall movements, and habitat use of hunted and non-hunted Ruffed Grouse in northern Michigan. Ph.D. Dissertation. Michigan State University, East Lansing, MI. 174 pp.
- Davies, R.G., and A.T. Bergerud. 1988. Demography and behavior of Ruffed Grouse in British Columbia. Pp. 78–121, *In* A.T. Bergerud, and M.W. Gratson (Eds.). *Adaptive Strategies and Population Ecology of Northern Grouse*. Volume II: Theory and Synthesis. University of Minnesota Press, Minneapolis, MN. 408 pp.
- DeGraaf, R.M., and M. Yamasaki. 2003. Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. *Forest Ecology and Management* 185:179–191.
- Dessecker, D.R., and D.G. McAuley. 2001. Importance of early-successional habitat to Ruffed Grouse and American Woodcock. *Wildlife Society Bulletin* 29:456–465.
- DeStefano, S., and D.H. Rusch. 1986. Harvest rates of Ruffed Grouse in northeastern Wisconsin. *Journal of Wildlife Management* 50(3):361–367.

- Devers, P.K., D.F. Stauffer, G.W. Norman, D.E. Steffen, D.M. Whitaker, J.D. Sole, T.J. Allen, S.L. Bittner, D.A. Buehler, J.W. Edwards, D.E. Figert, S.T. Friedhoff, W.W. Giuliano, C.A. Harper, W.K. Igo, R.L. Kirkpatrick, M.H. Seamster, H.A. Spiker, Jr., D.A. Swanson, and B.C. Tefft. 2007. Ruffed Grouse population ecology in the Appalachian region. *Wildlife Monographs* 168:1–36.
- Dobony, C.A., and R. Rainbolt. 2008. American Woodcock on Fort Drum Military Installation, New York. *Northeastern Naturalist* 15(2):241–248.
- Dorney, R.S., and C. Kabat. 1960. Relation of weather, parasitic disease, and hunting to Wisconsin Ruffed Grouse populations. Wisconsin Conservation Department Technical Bulletin 20. Wisconsin Conservation Department, Madison, WI. 64 pp.
- Edminster, F.C. 1937. An analysis of the value of refuges for cyclic game species. *Journal of Wildlife Management* 1(1–2):37–41.
- Edminster, F.C. 1954. The Ruffed Grouse. Pp. 195–242, *In* American Game Birds of Field and Forest: Their Habits, Ecology and Management. Charles Scribner's Sons, New York, NY. 490 pp.
- Ellison, L.N. 1991. Shooting and compensatory mortality in tetraonids. *Ornis Scandinavica* 22(3):229–240.
- Endrulat, E.G., S.R. McWilliams, and B.C. Tefft. 2005. Habitat selection and home-range size of Ruffed Grouse in Rhode Island. *Northeastern Naturalist* 12:411–424.
- ESRI. 2006. ArcMap Version 9.2. ESRI, Redlands, CA.
- Fearer, T.M. 1999. Relationship of Ruffed Grouse home-range size and movement to landscape characteristics in southwestern Virginia. M.Sc. Thesis. Virginia Polytechnic Institute and State University, Blacksburg, VA. 84 pp.
- Fearer, T.M., and D.F. Stauffer. 2004. Relationship of Ruffed Grouse, *Bonasa umbellus*, to landscape characteristics in southwest Virginia, USA. *Wildlife Biology* 10(2):81–89.
- Fielding, A.H., and J.F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24(1):38–49.
- Fischer, C.A., and L.B. Keith. 1974. Population responses of central Alberta Ruffed Grouse to hunting. *Journal of Wildlife Management* 35:585–600.
- Gullion, G.W. 1965. Improvements in methods for trapping and marking Ruffed Grouse. *Journal of Wildlife Management* 29:109–116.
- Heisey, D.M., and B.R. Patterson. 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. *Journal of Wildlife Management* 70(6):1544–1555.
- Henner, C.M., M.J. Chamberlain, B.D. Leopold, and L. Wes Burger, Jr. 2004. A multi-resolution assessment of Raccoon den selection. *Journal of Wildlife Management* 68(1):179–187.
- Hewitt, D.G., and R.L. Kirkpatrick. 1997. Daily activity times of Ruffed Grouse in southwestern Virginia. *Journal of Field Ornithology* 68(3):413–420.
- Hunyadi, B.W. 1984. Ruffed Grouse restoration in Missouri. Pp. 21–35, *in* W.L. Robinson (Ed.). Ruffed Grouse Management: State of the Art in the Early 1980s. North Central Section of the Wildlife Society, Bethesda, MD. 181 pp.
- Kaplan, E.L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* 53(282):457–481.
- Kunkel, K.E., and D.H. Pletscher. 2000. Habitat factors affecting vulnerability of Moose to predation by Wolves in southeastern British Columbia. *Canadian Journal of Zoology* 78(1):150–157.

- Lunn, M., and D. McNeil. 1995. Applying Cox regression to competing risks. *Biometrics* 51:524–532.
- McDonald, J.H. 2009. Fisher's exact test. Pp. 70–75, *In Handbook of Biological Statistics*, Second Edition. Sparky House Publishing, Baltimore, MD. 319 pp. Available online at <http://udel.edu/~mcdonald/statfishers.html>. Accessed 1 October 2009.
- McGarigal, K., S.A. Cushman, M.C. Neel, and E. Ene. 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available online at www.umass.edu/landeco/research/fragstats/fragstats.html. Accessed 1 December 2007.
- Migoya, R., and G.A. Baldassarre. 1995. Winter survival of female Northern Pintails in Sinaloa, Mexico. *Journal of Wildlife Management* 59(1):16–22.
- Mitchell, B.R. 2005. FragStatsBatch for ArcGIS 9. Computer software. Available online at <http://arcscripsts.esri.com/details.asp?dbid=13995>. Accessed 26 March 2008.
- Moser, J., J. Herron, B. Schongar, N. McBride, E. Haslun, J. McDermott, N. Channing, P. McLaren, B. Henry, D. Martin, T. Folts, and P. Haskins. 2001. Helderbergs Unit management plan: A management unit consisting of three state forests and three wildlife management areas in western and southeastern Albany County. New York State Department of Environmental Conservation, Albany, NY. 73 pp. Available online at http://www.dec.ny.gov/docs/lands_forests_pdf/helderbergsump.pdf. Accessed 1 October 2009.
- National Audubon Society, Inc. 2008. State of the birds. Common birds in decline: Ruffed grouse. Available online at <http://stateofthebirds.audubon.org/cbid/profile.php?id=20>. Accessed 15 April 2009.
- NYSDEC Habitat Inventory Unit. 1990. Ecological Zones—New York State. New York State Department of Environmental Conservation (NYSDEC), Albany, NY. Vector digital data. Available online at <http://www.nysgis.state.ny.us/gisdata/inventories/details.cfm?DSID=1131>. Accessed 19 October 2009.
- Palmer, W.L., and C.L. Bennett, Jr. 1963. Relation of season length to hunting harvest of Ruffed Grouse. *The Journal of Wildlife Management* 27(4):634–639.
- Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling* 133:225–245.
- Pollack, K.H., S.R. Winterstein, C.M. Bunck, and P.D. Curtis. 1989a. Survival analysis in telemetry studies: The staggered entry design. *Journal of Wildlife Management* 53(1):7–15.
- Pollack, K.H., S.R. Winterstein, and M.J. Conroy. 1989b. Estimation and analysis of survival distributions for radio-tagged animals. *Biometrics* 45(1):99–109.
- Post, T. 2008. Ruffed Grouse, *Bonasa umbellus*. Pp. 138–139, *In* K.J. McGowan and K. Corwin (Eds.). *Second Atlas of Breeding Birds in New York State*, Cornell University Press, Ithaca, NY. 688 pp.
- Roberts, S.D. 1993. Survival and reproduction of Wild Turkeys in south-central New York. M.Sc. Thesis. State University of New York College of Environmental Science and Forestry, Syracuse, NY. 81 pp.
- Roussel, Y.E., and R. Ouellet. 1975. A new criterion for sexing Quebec Ruffed Grouse. *Journal of Wildlife Management* 39:443–445.
- Rusch, D.H., and L.B. Keith. 1971. Seasonal and annual trends in numbers of Alberta Ruffed Grouse. *Journal of Wildlife Management* 35:803–822.
- SAS Institute Inc. 1999. SAS/STAT® User's Guide, Version 8. Cary, NC. 1464 pp.
- Sauer, J.R., J.E. Hines, and J. Fallon. 2008. The North American Breeding Bird Survey: Results and analysis 1966–2007. Version 5.15.2008. USGS Patuxent Wildlife Research Center, Laurel, MD.

- Servello, F.A., and R.L. Kirkpatrick. 1986. Sexing Ruffed Grouse in the Southeast using feather criteria. *Wildlife Society Bulletin* 14:280–282.
- Small, R.J., J.C. Holzward, and D.H. Rusch. 1991. Predation and hunting mortality of Ruffed Grouse in central Wisconsin. *Journal of Wildlife Management* 55:512–520.
- Thogmartin, W.E., and B.A. Schaeffer. 2000. Landscape attributes associated with mortality events of Wild Turkeys in Arkansas. *Wildlife Society Bulletin* 28(4):865–874.
- Thomas, D.L., and E.J. Taylor. 2006. Study designs and tests for comparing resource use and availability II. *Journal of Wildlife Management* 70(2):324–336.
- Thompson, F.R., III, and D.R. Dessecker. 1997. Management of early-successional communities in central hardwood forests: With special emphasis on the ecology and management of oaks, Ruffed Grouse, and forest songbirds. General Technical Report NC-195. US Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, MN. 33 pp.
- Whitaker, D.M., D.F. Stauffer, G.W. Norman, P.K. Devers, J. Edwards, W.M. Giuliano, C. Harper, W. Igo, J. Sole, H. Spiker, and B. Tefft. 2007. Factors associated with variation in home-range size of Appalachian Ruffed Grouse (*Bonasa umbellus*). *Auk* 124(4):1407–1424.
- White, G.C., and R.A. Garrott. 1990. *Analysis of Wildlife Radio-Tracking Data*. Academic Press, London, UK. 383 pp.
- Yoder, J.M., E.A. Marschall, and D.A. Swanson. 2004. The cost of dispersal: Predation as a function of movement and site familiarity in Ruffed Grouse. *Behavioral Ecology* 15:469–476.