TEMPORAL VARIABILITY IN SURVIVAL OF NON-BREEDING NORTHERN BOBWHITES IN OHIO

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ABSTRACT

Non-breeding season survival is an important determinant of population growth rates of northern bobwhites (*Colinus virginianus*) and is primarily influenced by hunter harvest, predation, and weather. The collective influence of these factors varies within and among years and across the bobwhite range. Understanding factors that influence variation in survival is important to inform regionally-specific management strategies for declining bobwhite populations. We radiomarked 311 bobwhites from 73 coveys to investigate temporal variation in non-breeding season (Oct-Mar) survival of a declining bobwhite population on private land in southwestern Ohio during 2008–2011. We used the data bootstrapping feature in Program MARK to adjust for overdispersion caused by dependency of survival among members of the same covey. Temporal variation in survival was best modeled ($w_i = 0.935$) with weekly differences in survival rates that varied within and between years. There was only slight dependency in survival due to covey affiliation between the 2 seasons (median $\hat{c} = 1.51$). Non-breeding season survival was low ($\hat{S}_{2009-2010} = 0.05$, 95% CI = 0.03-0.11, $\hat{S}_{2010-2011} = 0.12$, 95% CI = 0.07-0.20) in 2 years with data for the entire season. Survival during 10 December-31 March varied among the 3 years ($\hat{S}_{2008-2009} = 0.45$, 95% CI = 0.29-0.61, $\hat{S}_{2009-2010} = 0.11$, 95% CI = 0.05-0.21, $\hat{S}_{2010-2011} = 0.25$, 95% CI = 0.17-0.34). There were 2 periods of low survival; a short period in early fall that coincided with senescence of herbaceous vegetation and the hunting season, and during periods with prolonged snow cover during winter. Late winter survival during periods of snow cover was most variable and winter severity appeared to have the greatest influence on seasonal survival during our study. Management strategies to improve non-breeding season survival in northern populations should focus on managing winter habitat to improve survival during periods of prolonged snow cover.

INTRODUCTION

Life-history theory predicts changes in reproduction are most important for short-lived species with high fecundity and low survival (Stahl and Oli 2006). However, survival generally has more influence on growth rates of declining populations (Meats 1971). Demographic analyses support the relationship between survival and growth rates of declining populations of northern bobwhites and have established that non-breeding season survival is the most influential vital rate (Folk et al. 2007, Link et al. 2008, Sandercock et al. 2008, Gates et al. 2012). Variation in non-breeding season survival of northern populations strongly influences population viability (Guthery et al. 2000, Williams et al. 2003a), and management strategies need regional estimates of survival rates upon which to base conservation efforts (Brennan 1991, Cox et al. 2004).

Low non-breeding season survival is characteristic of bobwhite populations in northern parts of their range, but

sources of mortality and seasonal variation in survival are less well understood. Previous studies documented the influence of regionally-varying factors such as hunter harvest (Pollock et al. 1989b, Williams et al. 2004a, Rolland et al. 2010) or seasonal variation in weather (Roseberry and Klimstra 1984, Robel and Kemp 1997). The influence of these and other factors that affect non-breeding season survival vary across the species' range and under different management regimes (Williams et al. 2004b).

Seasonal and annual comparisons of survival require understanding of the precision of estimators through time. Variance of temporal survival estimates is affected by 2 factors: overdispersion and variability in sampling effort. Dependency between individuals in survival analyses produces overdispersion, which can misleadingly reduce variance estimates (Schmutz et al. 1995). Previous survival estimates reported for bobwhites from radio-telemetry studies have not explicitly addressed dependency in survival that arises from individuals in the same covey sharing resources and exposed to similar mortality factors (Williams et al. 2003b). Failure to address dependency can potentially provide biased estimates of variability in survival through the season (Schmutz et al.

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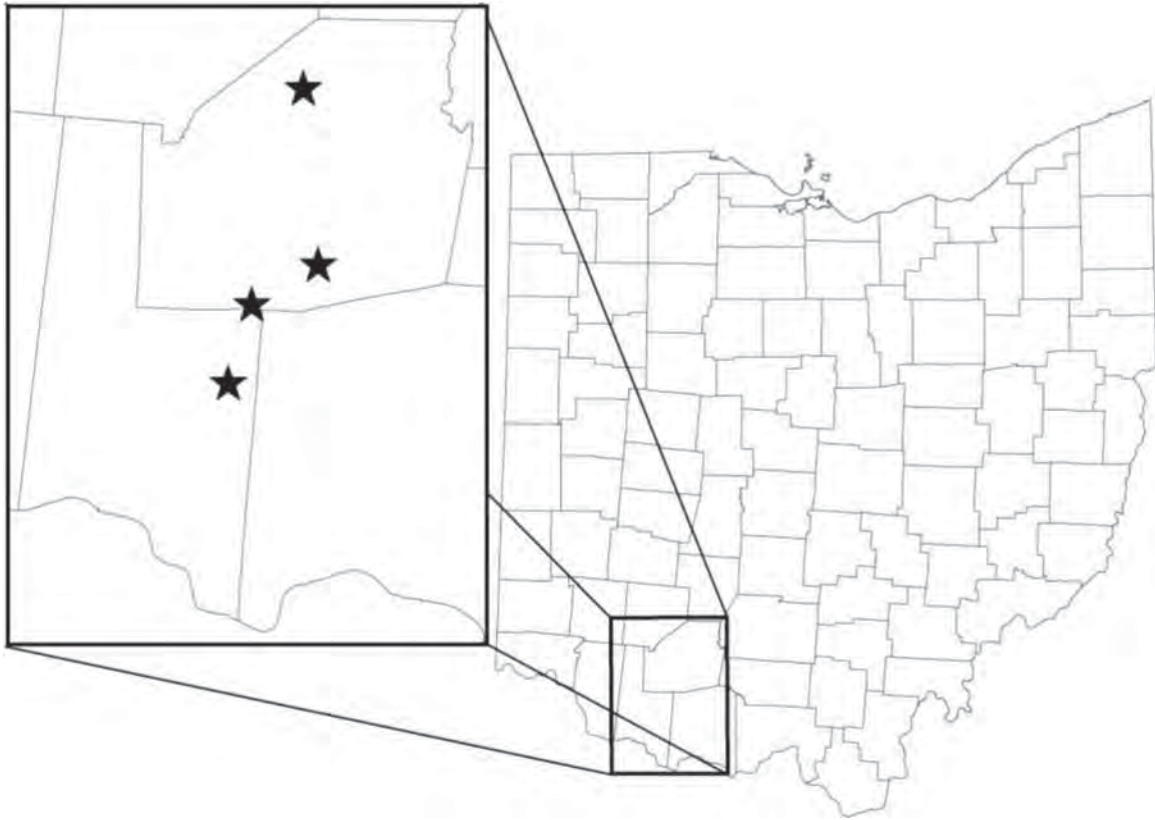
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Fig. 1.   Location of 4 private land study sites in Highland and Brown counties in southwestern, Ohio, USA.

1995). Inconsistent sampling effort throughout a study can also lead to imprecise variance estimates by confusing process variation with sampling variation (Burnham et al. 1987, Gould and Nichols 1998). Survival analyses can identify periods within seasons with low or highly variable survival rates by first addressing confounding influences of variation in sampling effort and non-independence. That information can be used to focus conservation efforts to improve survival and, ultimately, growth rates of declining populations (Gould and Nichols 1998, Moynahan et al. 2006).

We investigated temporal patterns of variation in non-breeding season survival of a bobwhite population near the northern periphery of the species' range. Our objectives were to: (1) compare the fit of temporal models to understand intra- and inter-seasonal non-breeding season survival and identify periods of lowest survival, and (2) test for overdispersion between covey members in survival analysis to improve variance estimates.

STUDY AREA

We conducted our study within the core bobwhite distribution in Highland and Brown counties (Spinola and Gates 2008) in southwestern Ohio (centered on 39° 04′ 59", 83° 39′ 10"; Fig. 1). Highland and Brown counties were in the glaciated till plains physiographic region (Ohio Division of Geologic Survey 1998). Primary land use in the region was agriculture, including 39% row crops and 17% pasture and hay (Homer et al. 2004). The region was mostly rural (6% developed). Woodlots and grasslands accounted for 33 and 3% of the landscape, respectively.

We worked on 4 private land study sites (400-1,200 ha) where bobwhite coveys were consistently found during the non-breeding season (Oct-Mar 2008–2011). Composition of the study areas was primarily row crop fields (55%) planted with soybeans and corn. Early succession vegetation, including fields enrolled in the Conservation Reserve Program (CRP), old fields, fence-rows, and agricultural drainage ditches collectively accounted for 19% of the area of the study sites. Grass fields were dominated by fescue (*Festuca* spp.) or planted warm season grasses, primarily Indiangrass (*Sorghastrum nutans*), big bluestem (*Andropogon gerardii*), and switch-grass (*Panicum virgatum*). Dominant forbs in grasslands were goldenrod (*Solidago* spp.), Queen Anne's lace (*Daucus carota*), and partridge pea (*Chamaecrista fasciculata*). Early succession woody vegetation was primarily blackberry (*Rubus allegheniensis*) or black raspberry (*R. occidentalis*). Woodlots accounted for 13% of the study area. Upland woodlots were dominated by oaks (*Quercus* spp.) and hickory (*Carya* spp.) whereas wet woodlots were characterized by ash (*Fraxinus* spp.) and black walnut (*Juglans nigra*).

Weather during the study was variable and generally more severe than long-term averages (Table 1). Timing and severity of weather varied among the 3 study years. The winter was relatively mild in 2008-09 with 2 short (7-

Table 1. Non-breeding season (Oct-Mar) weather summary from Dayton, Ohio, 90 km northwest of 4 private land study sites in southwestern Ohio (NCDC 2011).

Winter	Mean temp (°C)	Total snow (cm)	Days ≥ 5 cm[a]
2008–2009	9.2	48.5	16
2009–2010	8.5	101.6	31
2010–2011	8.5	67.3	41
30-year average[b]	10.5	67.5	19.8

[a] Number of days within season with ≥ 5 cm snow cover at the time of observation.

[b] 1977–1978 through 2007–2008.

12 days) periods of snow cover > 5 cm; total daily accumulation did not exceed 25 cm. The weather was mild during December 2009-January 2010 but a prolonged period (22 days) of deep snow accumulation and cold temperatures occurred during February 2010. Snow accumulation during this period exceeded 25 cm for 9 consecutive days. There was consistent snow cover > 5 cm during December 2010-January 2011 and little snow accumulation in February. The duration of snow cover was prolonged but depth did not exceed 25 cm.

METHODS

We captured bobwhites with baited funnel traps (Stoddard 1931) and targeted mist-netting (Wiley et al. 2012) during October-March 2008–2011. We attached an aluminum leg band and recorded age, gender, and body mass of each bird (Rosene 1969). We fit a subsample of individuals weighing >165 g with 6.6-g (≤ 4% body mass) necklace style radio transmitters (Advanced Telemetry Systems, Isanti, MN, USA). Transmitters were equipped with an 8-hr mortality sensor. All birds were released at the capture site within 30 min. Trapping, handling, and marking protocols were reviewed and approved by the Animal Care and Use Committee at Ohio State University (protocol # 2007A0228).

We tracked all radio-marked birds ≥ 6 days/week by homing and triangulation from short distances (< 25 m) (White and Garrott 1990). We immediately located the transmitter after detecting a mortality signal and identified cause of mortality from field sign observed at the recovery site (Einarsen 1956) and condition of the transmitter. We recorded the cause of mortality as predation, hunter harvest, investigator-caused (e.g., transmitter entanglement, trap mortality), other (e.g., vehicle collision, weather), or unknown.

We used the known-fates model with a logit link function in Program MARK to estimate survival rates (White and Burnham 1999). The known-fates model calculates maximum likelihood estimates of survival and allows comparisons of models with multiple parameters to estimate their effect on survival (Murray 2006). We generated encounter histories with daily intervals for all birds that survived a 7-day post-capture exclusion period to control for short-term acute effects of capture and radiomarking (Guthery and Lusk 2004, Holt et al. 2009).

We excluded data from the first year of the study in the primary survival analyses because there were few birds radiomarked during 1 October to 9 December.

We compared *a priori* models to examine the appropriate temporal scale for seasonal variation in survival rates. Baseline temporal models tested for weekly, bi-weekly, monthly, and constant variability throughout the season. We also compared 2 models with linear and quadratic trends through the season. We evaluated each model (excluding the null model) with an additive and an interaction year term because we had no *a priori* prediction about differences in survival among years. We used the information theoretic approach to compare support for each model, based on Akaike Information Criterion adjusted for small sample sizes (AIC_c), and considered models with ΔAIC_c scores ≤ 2.0 to have equivalent support (Anderson and Burnham 2002). We added additional parameters to the best fitting temporal model to test for differences in age and gender and reported the relative influence of each parameter based on model coefficients and 95% confidence intervals.

We calculated survival of individuals captured in the first year of the study for a shortened interval (10 Dec-31 Mar) with the best fitting temporal model. We estimated survival for the same interval in each of the 2 full years with a shortened encounter history to make comparisons among the 3 seasons.

We used an intercept only random effects model to estimate process variance with the variance components analysis in Program MARK (Burnham et al. 1987, Gould and Nichols 1998, White et al. 2001). We compared the ratio of sampling and process variances for the 2 years and report the estimate of process variance. Sampling variance is an estimate of variability in the parameter that includes variation in sampling effort and natural processes. Process variance removes the sampling variability from the estimate to provide a more precise estimate of the true variation in the population parameter.

We used the bootstrap procedure in Program MARK to estimate an overdispersion parameter (c) to test for dependency in survival among covey members (Bishop et al. 2008). Overdispersion parameters, or variance inflation factors, adjust variance estimates to more correctly model overdispersed data (Schmutz et al. 1995, Anderson and Burnham 2002). The general approach for estimating c is to divide the goodness-of-fit statistic of the model with the most parameters by the degrees of freedom of that model (Anderson and Burnham 2002). However, this approach is sensitive to sample sizes and fails to explicitly consider the cause of overdispersion.

Data bootstrapping can be used to estimate c when the source of dependency is known (Bishop et al. 2008). A common example of known sources of dependency is siblings, where ≥ 2 individuals in the survival analysis have the same maternal resources and are exposed to similar environments and mortality sources. The bootstrapping procedure resamples from known groups (e.g., siblings or coveys), rather than by individual encounter histories, to generate survival estimates. The overdispersion parameter ($\hat{c}$) is calculated as $\hat{c} = SD(\hat{S})^2/SE(\hat{S})^2$

Table 2. Selection for candidate models to explain inter- and intra-seasonal variation in non-breeding season (Oct-Mar) survival of northern bobwhites in southwestern Ohio, 2009–2011.

Model	AIC_c[b]	ΔAIC_c[b]	w_i[b]	k[b]
Week + Year+Week x Year	1585.479	0.000	0.935	52
BiWeek + Year+BiWeek x Year	1590.822	5.343	0.065	26
Month + Year+Month x Year	1617.168	31.689	0.000	12
Week	1654.372	68.894	0.000	26
Week + Year	1655.735	70.256	0.000	27
BiWeek	1674.825	89.347	0.000	13
BiWeek + Year	1676.236	90.757	0.000	14
Month	1678.458	92.979	0.000	6
Month + Year	1680.189	94.711	0.000	7
tt + Year+tt x Year	1680.235	94.757	0.000	6
t + Year+t x Year	1692.596	107.118	0.000	4
tt	1693.162	107.683	0.000	3
tt + Year	1694.938	109.459	0.000	4
Constant	1697.542	112.064	0.000	1
Constant + Year	1698.906	113.428	0.000	2
t	1699.384	113.906	0.000	2
t + Year	1700.785	115.307	0.000	3

[a] Temporal effects modeled as constant through year, linear time trend (t), quadratic time trend (tt), and weekly, bi-weekly, and monthly periods.
[b] AIC_c = Akaike's Information Criterion adjusted for small sample sizes, ΔAIC_c = difference between AIC_c of best fitting and current model, w_i = Akaike's weight, k = number of parameters in model.

where $SD(\hat{S})$ is the standard deviation of bootstrapped survival estimates and $SE(\hat{S})$ is the standard error of the survival estimate from the maximum-likelihood analysis (Bishop et al. 2008).

We generated 10,000 estimates of $\hat{S}$ with the most parsimonious temporal model ($\Delta AIC_c < 2$ and fewest parameters). Using the best fitting temporal model removes variability that could be misinterpreted as overdispersion. The procedure removed individuals from randomly selected coveys and estimated $\hat{S}$ for the subset of data during each iteration (Bishop et al. 2008). Total sample size for each iteration depended on the number of radio-marked individuals in each covey in the subset data. Covey affiliation was specified as an individual covariate in the encounter history. We used the median $\hat{c}$ estimate from the 2 years in the bootstrapping analysis to approximate the variance inflation factor for the study (Anderson and Burnham 2002). We considered over-dispersion to be present in the data if the $\hat{c}$ estimate was >1.2 as an *a priori* rule (Bishop et al. 2008).

A covey was defined as ≥ 2 individuals that were together for ≥ 7 consecutive days. Some investigators have reported dynamic covey affiliation among individuals through the non-breeding season (Yoho and Dimmick 1972, Williams et al. 2004a), but individuals rarely changed covey affiliations during our study (Janke 2011). We identified the resulting group when 2 formerly unique coveys combined as a unique covey in the analysis, right-censored individuals in the covey, and re-entered them in the risk set as a new individual with the combined covey.

There was a 23-day hunting season with a 4 bird bag limit during the last 3 weeks of November each year. We did not restrict or influence hunter effort or access on any of the sites. We distributed log books to hunters and landowners on each site to monitor hunting effort and success. We calculated a cumulative incidence function (CIF) to estimate cause-specific mortality related to hunter harvest to measure the contribution of harvest to non-breeding season mortality (Heisey and Patterson 2006). The cumulative incidence function calculates the relative influence of a specific mortality factor on survival in a population exposed to multiple risk factors (in addition to the factor[s] of interest, i.e., harvest.). This approach uses the staggered entry design of the Kaplan Meier estimator (Pollock et al. 1989a) to generate survival estimates and cause-specific mortality rates sensitive to problems of staggered entry (individuals that die early are not available for capture later in the study and affect differential survival rates through the season with variable sample sizes). The CIF approach also respects the property of 'conservation of mortality' raised by the existence of multiple mortality sources (Heisey and Patterson 2006: 1545). We used the wild1 package in R to calculate the CIF for harvest with data from all individuals surviving the 7-day exclusion period during the last 2 years of the study (Sargeant 2011).

Table 3. Survival estimates from maximum likelihood and bootstrapping procedures in the known-fates model in Program MARK for radio-marked northern bobwhites during the non-breeding season (Oct-Mar), 2009–2011.

Year	Maximum likelihood		Bootstrap		$\hat{c}$[a]
	$\hat{S}$	$SE(\hat{S})$	$\bar{\hat{S}}$	$SD(\bar{\hat{S}})$	
2009–2010	0.055	0.021	0.058	0.028	1.84
2010–2011	0.121	0.033	0.122	0.036	1.18

[a] Variance inflation factor; estimated by $SD(\hat{S})^2/SE(\hat{S})^2$.

Fig. 2. Daily survival estimates (Ŝ) and 95% CI for northern bobwhites over weekly intervals during the non-breeding season (1 Oct–31 Mar) in Ohio, 2008–2011. The lower line represents average snow depth (cm) from a regional weather station in Dayton, Ohio (90 km northwest of the sites) for each weekly

RESULTS

We included 311 bobwhites in survival analyses after a 7-day exclusion period (55 in 2008–2009, 130 in 2009–2010, and 126 in 2010–2011). The sample comprised 75% juveniles with slightly more males (54%) than females (46%). Five individuals were censored due to investigator-caused mortalities and 27 were censored due to radio transmitter failure. We included 256 individuals from 2 years (2009–10 and 2010–11) in the temporal analysis. All daily intervals in the analysis had $\geq$ 3 radio-marked birds and the mean ($\pm$ SD) number of radio-marked individuals per daily interval was 31 $\pm$11.1 (range = 3–60).

We identified 73 coveys (15 in 2008–2009, 27 in 2009–2010, and 31 in 2010–2011). Two coveys joined and were identified as a new covey on 2 occasions in 2009–2010 and 4 occasions in 2010–2011. The mean ($\pm$ SD) number of radio-marked individuals in each covey was 4.6 $\pm$ 2.3. The mean ($\pm$ SD) number of radio-marked individuals/covey/day was 2.3 $\pm$ 0.8.

The best fitting temporal model included weekly effects and the interaction of week with year (Table 2). There was little support for other temporal models, but the high ranking of heterogeneous models (biweekly and monthly models) with the annual interaction term indicated there was substantial inter- and intra-annual variation in survival. Additional covariates for gender and age did not improve model fit and were not included in the final model. There was no difference in survival between genders ($\beta_{Female} = 0.044$, 95% CI = - 0.278-0.367). Adults generally had higher survival than juveniles ($\beta_{Adult} = 0.286$, 95% CI = - 0.093-0.665) although models without age effects had equivalent support and the confidence interval for the age coefficient contained zero. The ratio of the standard error of process variance to observed variance in weekly survival intervals was 1, indicating the observed variation in survival was not attributable to differential sampling effort across weeks. The boot-strapping analysis revealed there was modest overdispersion in the data due to dependency between covey mates (Table 3; median $\hat{c} = 1.51$).

Non-breeding season survival estimates were low each year ($\hat{S}_{2009-2010} = 0.055$, 95% CI = 0.026-0.113, $\hat{S}_{2010-2011} = 0.121$, 95% CI = 0.069-0.203). Survival rates during 10 December- 31 March were variable among the 3 years ($\hat{S}_{2008-2009} = 0.449$, 95% CI = 0.295-0.613, $\hat{S}_{2009-2010} = 0.114$, 95% CI = 0.059-0.217, $\hat{S}_{2010-2011} = 0.247$, 95% CI = 0.170-0.345). Daily survival rates consistently declined through the non-breeding season and the lowest estimates occurred during December-February (Fig. 2). Periods of lowest survival coincided with increases in regional snow cover. Fall survival (Oct-Nov) was lower than other snow-free periods and the highest survival rates occurred in March.
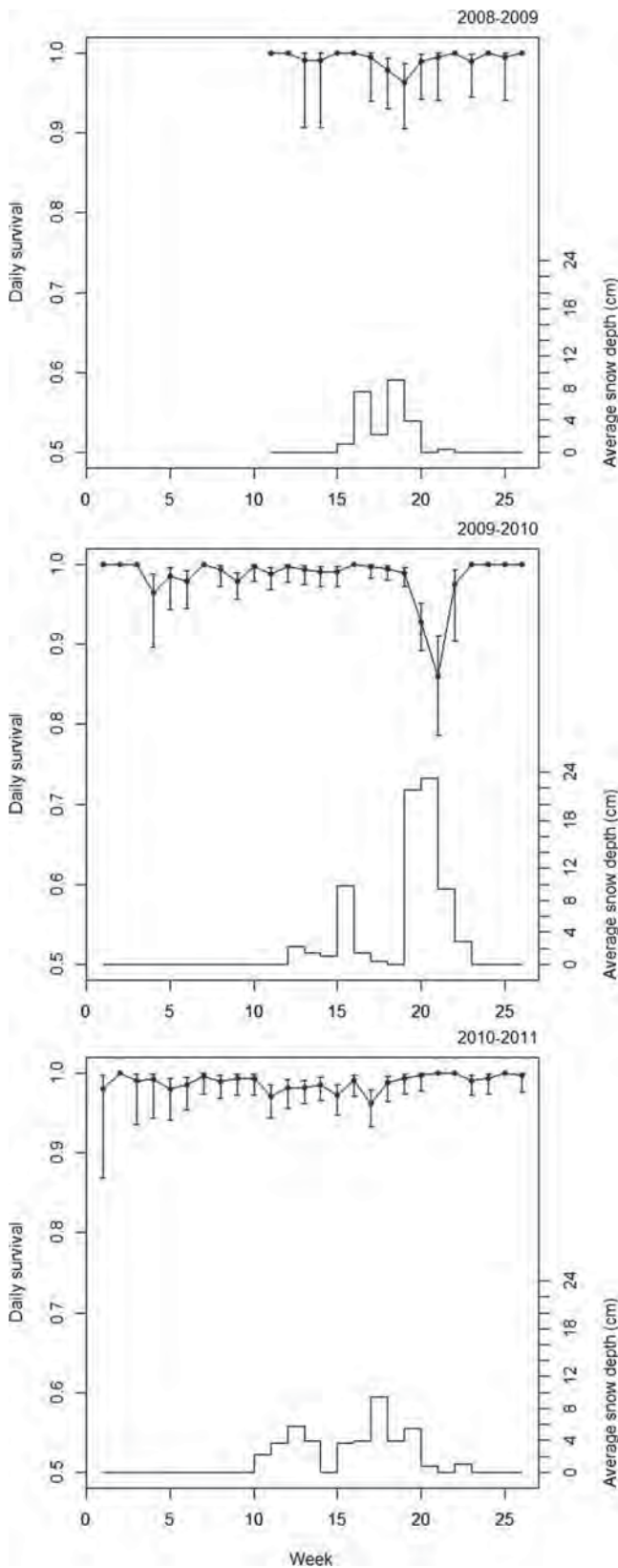
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interval (NCDC 2011). Daily snow observations within sites during 2009–2011 correlated with regional observations from the Dayton station, but were not available for the entire study period (Janke 2011).

Table 4. Inferred mortality causes from evidence at recovery locations of radio-marked northern bobwhites ($n = 186$) during the non-breeding season in southwestern Ohio, 1 October–31 March 2008–2011.

Cause	%
Hunter harvest	5.4
Investigator[a]	2.7
Other	1.1
Predation	
Avian	23.7
Mammalian	16.1
Unclassified	38.7
Unknown	10.2
Weather	2.2

[a]Capture or transmitter-related mortality.

Predation was the primary cause of mortality (78.5%), and avian predators were implicated in a majority of predation events (Table 4). Avian predators were also suspected in a majority of mortality cases recorded as unclassified predation, although evidence at the recovery site was insufficient to directly implicate avian predators. We confirmed predation by red (*Vulpes vulpes*) or gray (*Urocyon cinereoargenteus*) fox, mink (*Neovision vision*), feral cats (*Felis catus*), Cooper's (*Accipiter cooperii*), and sharp-shinned (*A. striatus*) hawks. We documented 13 hunting parties during 2009–2011 with hunter log books and observations in the field. Only 8 (6 in 2009-10, 2 in 2010-11) of 105 (57 in 2009-10, 48 in 2010-11) bobwhites radiomarked during the season were harvested. The CIF for harvest related mortality was 0.068 (95% CI = 0.012-0.123).

DISCUSSION

Survival is an important determinant of growth rates in bobwhite populations, and non-breeding season survival has been identified as the most important vital rate for populations near the northern extent of their range (Folk et al. 2007, Gates et al 2012). Weekly survival rates during our study were dynamic and appeared to be most influenced by snow accumulation, which led to low non-breeding season survival. The ratio of process variance to sampling variance in our analysis indicated weekly survival estimates were robust to variation in sampling effort and the data bootstrapping procedure showed that variance was not heavily influenced by dependency among covey members.

Covey affiliation was mostly static during our study (Janke 2011), which we predicted would result in high dependency among individuals in the same covey (Williams et al. 2003b). However, dependency among individuals was modest, likely because of consistently low survival rates documented across the entire population, driven primarily by severe winter weather. Dependency may be higher in populations subject to less widespread mortality factors (e.g., local variation in habitat quality, hunting pressure). The presence of $\hat{c} > 1.2$ does, however, show that covey-mates in our analysis

were not entirely biologically independent as assumed in survival analyses. Thus, model selection in future analyses may consider using the data bootstrapping procedure to estimate $\hat{c}$ (Bishop et al. 2008).

Comparison of temporal variation in survival assumes that any bias associated with radio transmitters is constant within and among seasons. Increased energy demands and diminished food availability during winter may lower body mass (Robel and Linderman 1966, Roseberry and Klimstra 1971) and negatively affect survival of radio-marked birds by increasing the proportional weight of transmitters relative to body mass (Johnson and Berner 1980, Burger et al. 1991). Janke (2011) found that body mass of radio-marked bobwhites in our study did not consistently decline during periods of snow cover, suggesting inferences from radio-marked birds during periods of snow cover are likely not negatively biased relative to other periods within the season or among years. Comparisons among intervals in our study and with previous radiotelemetry studies should still be valid, despite the potential for a systematic bias caused by transmitters (Guthery and Lusk 2004).

Variation in survival among years in our study was consistent with the variable non-breeding season survival estimates reported in an 11-year study in Oklahoma (Cox et al. 2004). Thus, within-season variation in mortality factors can have strong influence on seasonal survival rates and, ultimately, population growth rates. Estimates from the 3 seasons included in our analysis suggest variation in winter severity was the primary factor affecting non-breeding season survival. Winter survival was highest during 2008–2009 when snow accumulation and temperatures were closest to long-term averages, while survival during the severe winter of 2009–2010 was among the lowest estimates reported in the literature (Sandercock et al. 2008). Weekly survival rates declined considerably in association with snow accumulation in the region. The influence of severe winter weather on inter-seasonal population estimates was previously established by Roseberry and Klimstra (1984) and Robel and Kemp (1997) in Illinois and Kansas, respectively. Lohr et al. (2011) used radiotelemetry to estimate survival in a population near the northern portion of the bobwhite's range and reported comparatively high non-breeding season survival during 2 mild winters (Lohr 2009). The co-ocurrence of snow accumulation and low weekly survival rates in our study corroborates the link between winter severity and low non-breeding season survival in northern populations.

Errington and Hamerstrom (1935) reported the 2 primary periods affecting non-breeding season survival of bobwhites in northern populations were coincident with senescence of herbaceous vegetation and crop harvest in early fall and snow accumulation during winter. Winter survival was most variable during periods of snow accumulation in our study, and we documented a similar decline in fall survival during the hunting season and crop harvest. The co-occurrence of crop harvest and hunting season limited our ability to separate influences of each on observed survival. A high proportion of the study sites was in corn and soybeans, which were harvested during

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mid to late fall; thus, significant changes in distribution of suitable cover occurred over a short period. Bobwhites in agricultural landscapes use crop fields through the summer (M. R. Liberati, unpublished data; Potter et al. 2011) and crop harvest causes a rapid loss of usable habitat (Errington 1934, Guthery 1997). Reduced availability of usable habitat combined with senescence of herbaceous vegetation during this period likely contributed to the observed decrease in survival.

Hunting mortality has been identified as a primary factor affecting non-breeding season survival of bobwhites in Missouri (Burger et al. 1995), Oklahoma (Cox et al. 2004), and Florida (Rolland et al. 2010). Harvest during the short hunting season in our study appeared to influence weekly survival rates, but our estimates of cause-specific mortality for harvest-related mortality were lower than previously reported rates in populations exposed to hunting pressure (Burger et al. 1995, Cox et al. 2004). The collective influence of low fall survival had little influence compared to that exerted by severe winter weather.

MANAGEMENT IMPLICATIONS

Management strategies directed at increasing bobwhite population growth rates in Ohio should focus on increasing low non-breeding season survival because of its disproportional influence on population growth rates (Sandercock et al. 2008, Gates et al. 2012). Non-breeding season habitat management should specifically focus on microhabitats associated with increased survival during periods of snow accumulation (Roseberry 1964). Further research in northern portions of the bobwhite range should investigate the specific influence of winter weather and habitat quality on daily survival rates to identify appropriate management actions to improve survival.

ACKNOWLEDGMENTS

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