

Impact of harvest on survival of a heavily hunted game bird population

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Abstract

Context. Despite their economic importance and intensive management, many game bird species, including the northern bobwhite *Colinus virginianus*, are in decline. Declines may be explained, at least in part, by low survival due perhaps to poor habitat quality, high predation or excessive hunting pressure.

Aims. This study sought to estimate and model annual/seasonal survival probabilities, to evaluate factors influencing them and to determine the cause-specific mortality rates for northern bobwhites subject to varying levels of harvest on the Babcock–Webb Wildlife Management Area (BW area), south Florida, USA.

Methods. We applied Cox's proportional hazard models to data collected from 2066 radio-tagged bobwhites during 2002–2008 to test for intrinsic and extrinsic factors affecting survival and the non-parametric cumulative incidence function estimator to estimate cause-specific mortality rates.

Key results. Mean annual survival (0.091 ± 0.006) in the BW area was lower than most estimates reported for other bobwhite populations. Annual survival differed between adults (0.111 ± 0.008) and juveniles (0.052 ± 0.008), and varied among years. Survival in winter (October–March; 0.295 ± 0.014) was similar to that in summer (April–September; 0.307 ± 0.013). Density of food strips (i.e. long and narrow food plots) did not influence survival, but hunting effort (number of hunters per day per km²) had a substantial negative impact on survival. In the lightly hunted field trial zone, winter (October–March) survival was significantly higher (0.414 ± 0.035) than in the other more heavily hunted management zones (0.319 ± 0.016). Cause-specific mortality analyses revealed that bobwhite mortality during summer (April–September) was mainly due to raptor (39.7%) and mammalian predation (35.6%), whereas hunting was the primary cause of mortality during winter (47.1%).

Conclusions. Our results highlight the potential role of harvest as an important cause of the northern bobwhite population declines in south Florida. High mortality during winter may reduce recruitment of juveniles to the reproductive segment of the population, and ultimately the population growth.

Implications. Our results suggest that reduction in hunting pressure may be necessary to reverse the declining population trends in heavily hunted game species in public lands, such as the northern bobwhites in the BW area.

Introduction

The northern bobwhite quail, *Colinus virginianus* (hereafter bobwhites), an economically important game species in the south-eastern United States of America (Burger *et al.* 1999), has declined dramatically throughout most of its range (Sauer *et al.* 2008), primarily because of habitat loss and fragmentation (Dimmick *et al.* 2002). In public lands, hunting pressure is intense. In the Babcock–Webb Wildlife Management Area (BW area), a large but isolated state-owned land in south-west Florida, USA, annual harvest records suggest that the bobwhite population has substantially declined since the 1980s (R. Dimmick, pers. comm.). Despite intensive habitat management using techniques including roller-chopping

(chopping brushes with rotating blades mounted on drums), prescribed fires and food strips (long, narrow food plots), this population has continued to decline. This raises the possibility that overharvest caused, or contributed to, observed population declines; this, however, has not been thoroughly assessed.

A challenging issue in management of harvested populations is to determine whether mortality due to exploitation is additive to natural mortality, or is partially/totally compensatory. Under the hypothesis of compensatory mortality, originally developed from studies of bobwhites, it is assumed that there is a surplus of animals that, if not harvested, would die from other causes. This surplus could thus be harvested without negatively affecting population size (Errington 1945). Compensation generally

occurs as a result of density-dependent feedback at high densities. Conversely, the additive mortality hypothesis states that harvest mortality is additive to natural mortality, which reduces the overall survival rate. The concept of compensatory mortality is the basis of sustainable harvest theory and has been used to set harvest levels for many species (e.g. Smith *et al.* 1993). Thus, if hunting mortality is compensatory, managers may need to know the threshold of harvest rate above which the population would be adversely affected. A direct evaluation of the relationship between survival or abundance and hunting effort may help determine this threshold.

Mortality rates may vary annually and/or seasonally, and be influenced by several intrinsic factors such as age and sex, and extrinsic factors such as food resources and management actions. Short-lived birds such as bobwhites are characterised by low annual survival and high fecundity. In such species, adult survival is expected to have a higher annual variability than reproductive parameters (Saether and Bakke 2000). Furthermore, game birds may be exposed to different mortality factors throughout the year. Hunting generally occurs during a limited period, while predation risk may be higher during the breeding season. The bobwhite is a dimorphic species. Conspicuous males defend a territory, compete for females with vocal displays, and may incubate a nest when females lay and incubate another clutch. Thus, being involved in different reproductive activities, males may incur a different level of predation risk than females (Magnhagen 1991). Also, juveniles, being smaller, underdeveloped and inexperienced are likely to experience a higher mortality than adults (Roff 1992).

Understanding the relative influence of habitat quality and hunting pressure on demographic parameters and population dynamics is crucial for effective management of game species. The impact of hunting pressure on season-, age- and sex-specific survival must be determined. Also, effect on survival of existing management actions such as food supplementation (e.g. feeders or food plots) and predator control needs to be evaluated since they may be inefficient or have unexpected negative effects (Bro *et al.* 2004; Evans 2004).

Most previous studies have evaluated the hunting impact on game bird populations by comparing cause-specific mortality rates (Burger *et al.* 1995; Alonso *et al.* 2005; Robinson *et al.* 2009) or survival among areas with varying degrees of hunting pressure (Smith and Willebrand 1999; Devers *et al.* 2007). Few studies have explicitly modelled survival as a function of hunting effort (e.g. Otis 2002). In this study, we focussed on evaluating the direct impact of hunting effort on bobwhite survival in the BW area. We intensively monitored radio-tagged bobwhites for 7 years, and used these data to (1) estimate survival probabilities, (2) test for annual/seasonal variation, and sex- and age-specific differences in survival probabilities, (3) assess the effect of hunting pressure on bobwhite survival, and (4) quantify annual and seasonal cause-specific mortality rates.

Material and methods

Study species and sites

Northern bobwhite quails are small (140–170 g) and short-lived (on average less than one year) land birds (Brennan 1999). During the breeding season, clutches of 12 eggs on average (range 5–18)

are incubated for 23 days, and the first peak of hatching occurs between late May and mid-June. Renesting is common. After the breeding season, adults and juveniles of both sexes gather in coveys (group of usually 12–15 individuals) to overwinter. Hunting generally occurs during this period. Bobwhites are exposed to predation throughout the year, and common predators include raptors (several species of hawks and owls), mammals (e.g. grey fox (*Urocyon cinereoargenteus*), raccoons (*Procyon lotor*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*)) and snakes.

The study was conducted in the Babcock–Webb Wildlife Management Area (26 799 ha), Charlotte County, in south-west Florida (Fig. 1). The most significant plant communities included dry prairie, pine–palmetto and wet prairie (Singh *et al.* in press). The area is subject to periodic short-duration flooding and prolonged drought. Prescribed burning in the dormant season, roller-chopping and *Sesbania* sp. food strips (composing 0.56% of the total area) are currently the primary habitat management activities. The BW area is divided into five management zones: A (6342 ha), B (6258 ha), C (5396 ha), D (5689 ha), and a field trial course F (3132 ha; Fig. 1). The spatial density of food strips, constant over the study period, was 30.81, 39.77, 49.22, 52.25 and 161.24 m² per ha in zones A, B, C, D and F, respectively. The first four zones (A, B, C and D) are open to hunting from mid-November to late December, whereas in the field trial area (F), hunting is permitted for only 2 days in late January (for a maximum of 25 hunters each day). The daily bag limit was set at six quail per hunter for every zone. However, zones A and B were designated as limited access (10 hunters per day) whereas access to zones C and D was unlimited, with zone C by far preferred by hunters.

Field methods

Birds were captured between October 2002 and March 2009 with baited funnel traps. Birds were weighed to the nearest gram, aged, sexed, and leg-banded. Those weighing at least 130 g were radio-marked with a 6-g necklace-style transmitter with a mortality

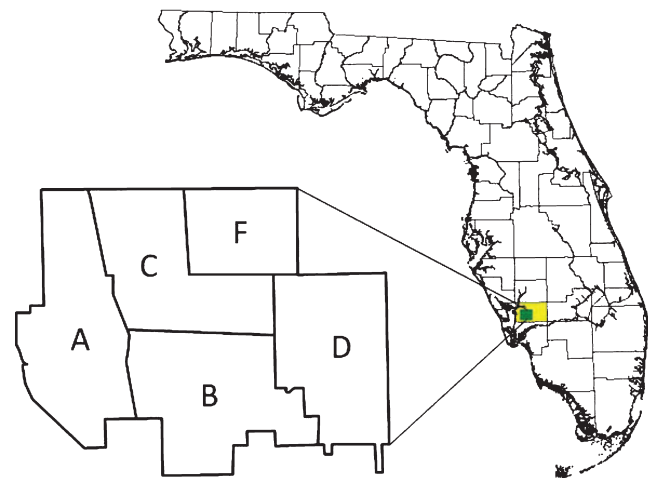


Fig. 1. Location of the Babcock–Webb (BW) Wildlife Management Area, Charlotte County, south Florida, USA. The area is divided into five management zones (A, B, C, D and F) with different levels of hunting pressure and food strip density (see text for details).

sensor (American Wildlife Enterprises, B. Mueller, Monticello, FL), and tracked until death or censoring. Antenna length was 22 cm. Transmitters had an expected battery life of 365 days and a signal range of ~500 to 1000 m in the BW area. Individual bird locations were attempted at 3–5 day intervals. Radio-marked birds were located using hand-held receivers and Yagi antennas. Cast nets ~3 m in diameter were used to capture unmarked birds that were associated with radio-tagged birds. Birddogs helped to locate new birds not associated with radio-tagged birds. Birds missing for several days were located with a truck-mounted whip antenna. When a mortality signal was received, the bird was immediately located and probable cause of death determined. During the hunting season, we searched for unrecovered injured or dead radio-marked birds every 2 days. All trapping and handling protocols were approved by the University of Florida Institutional Animal Care and Use Committee (protocol number A-794).

Survival analysis

In total, 2066 radio-tagged individuals (745 females and 1321 males) were used in the survival analyses; 499 of them were right-censored because birds lost their radio-collars or the radio-collars failed. Sex ratio was biased for adults (sex ratio of females to males of 0.48) but not for juveniles (sex ratio of 0.93). We used Cox's proportional hazard models with the *coxph* procedure implemented in the *survival* package of the R software (R Development Core Team 2008). Tied failure times were handled with the 'Efron' method and we chose the Kaplan–Meier option for the baseline function (Therneau and Grambsch 2000).

We considered a quail year to be from 1st of October of year t to the 30th of September of year $t+1$. We thus analysed annual survival, for the period 2002–2007, by using the following stepwise approach. We first tested for the additive and interactive effects of age class (juveniles: birds hatched in summer of year t ; and adults: birds hatched all previous years), sex (males and females) and year. Model comparison was performed with the Akaike's Information Criterion (AIC). When the difference in AIC value exceeded two, the best model was the model with the lowest AIC. Otherwise, models were assumed to be not different and we selected the (most parsimonious) model with the lowest number of parameters (Burnham and Anderson 2002). Point estimates \pm s.e. are provided.

Next, we used the most parsimonious model from the preceding analyses to test for (1) the additive and interactive effects of *Sesbania* food strip density (FSD), and (2) the effect of hunting pressure in two ways. First, we tested for the 'Zone' effect (A, B, C, D and F; see 'study species and sites' for details). Second, since Cox's models permit estimation of daily survival, we modelled survival as a direct function of hunting effort defined as the number of hunters per day per km² in each zone for each hunting season (i.e. around 40 days in zones A, B, C, D and 2 days in F). We note that hunting effort was highly correlated with harvest effort (i.e. number of quails harvested day⁻¹ km⁻²; $r^2 = 0.867$, $P < 0.001$).

In addition to annual survival, we also analysed seasonal survival because mortality factors may vary seasonally and

also because hunting occurred only from November to January. We considered the period from the 1st of October to the 31st of March as *winter season*, and the period from the 1st of April to the 30th of September as *summer season*. Thus, we had adequate data to analyse winter survival for the period 2002–2008, and summer survival for the period 2003–2008. Because survival estimates were based on different (summer and winter) datasets, an AIC-based approach was not appropriate for comparing summer and winter survival. Thus, to test for a difference in survival between summer and winter seasons, we used the program CONTRAST, which allows comparison of multiple survival estimates (Hines and Sauer 1989). Then, we analysed summer and winter survivals separately, following the same approach as previously described for annual survival, but without tests for the effect of hunting on summer survival.

Statistical inferences were based on an information-theoretic approach (using the AIC and the AIC weights). Tests of proportional hazard assumption (Therneau and Grambsch 2000) revealed no violation, except for the zone effect. This is not surprising since harvest occurred at different times and durations in different zones. We thus estimated annual, winter and summer survival for each zone with the Kaplan–Meier staggered-entry method (Pollock *et al.* 1989b) using the procedure *survfit* also available in the R *survival* package and then used CONTRAST software to test for an overall zone effect on these estimates and to perform *post hoc* tests when the overall comparison was significant.

Cause-specific mortality

Based on field evidence and recovered radio-transmitters, each known mortality event was assigned to one of five categories: (1) harvest; (2) predation by raptors; (3) predation by mammalian predators; (4) other; and (5) unknown causes. Although we believe that the cause of mortality was accurately determined, we cannot rule out the possibility of some confusion due to postmortem scavenging of carcasses in some cases. Cause-specific mortality rates were estimated using the non-parametric cumulative incidence function estimator (Heisey and Patterson 2006). Because the proportional hazard assumption was not met with the management zone as a covariate, we could not use the stratified Cox proportional hazard models to test for difference in cause-specific mortality rates between management zones A, B, C and D and zone F. We thus used the CONTRAST software to compare cause-specific mortality rates among management zones.

Results

Annual survival

Average annual survival was 0.091 ± 0.006 and varied among years (Fig. 2). Annual survival was not significantly different among zones ($\chi^2(4) = 5.077$, $P = 0.280$, Table 1). The two highest ranked models indicated that annual survival varied among age classes and years with no convincing evidence of a sex effect (models 7 and 8, Table 2). We chose the model with the additive effect of age classes and years (model 7, Table 2) for further analysis because this model had fewer parameters, and also because survival of adults and juveniles varied similarly

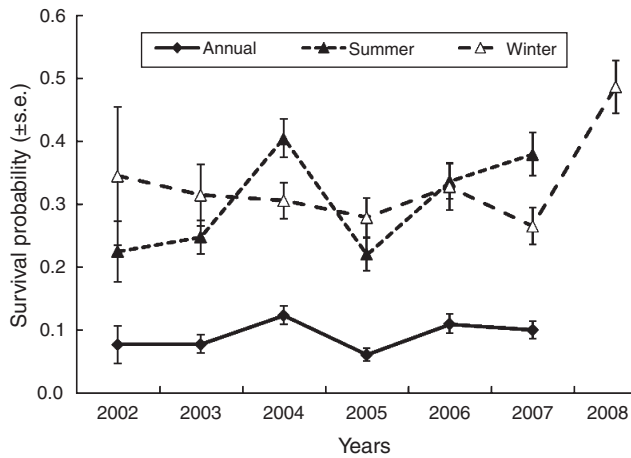


Fig. 2. Year-to-year variations in annual (October–September), winter (October–March) and summer (April–September) survival (estimated from Cox’s models with year as a covariate) of bobwhites in BW area, south Florida, USA. Error bars indicate ±s.e.

during the study period (Fig. 3). Overall, adults had a higher mean annual survival than juveniles (0.111 ± 0.008 and 0.052 ± 0.008 , respectively).

Using the model with an additive effect of age class and year as the base model, we tested for the effects of food strip density (FSD) and hunting effort. There was no evidence that FSD influenced annual survival (Table 3). On the other hand, there was strong evidence that hunting effort substantially negatively affected annual survival (risk ratio: 26.01) but its influence varied among years (model 5, Table 3). Survival of birds in the management zone F, where hunting effort was the lowest, was the least affected by hunting effort. Conversely, management zone C, where hunting effort was the highest because of higher hunter preference permitted by easier access, exhibited the lowest survival. Survival of birds in management zones A, B and D was intermediate.

Seasonal variation

Summer survival (0.307 ± 0.013), although slightly higher, did not significantly differ ($\chi^2 = 0.391$, d.f. = 1, $P = 0.532$) from

Table 1. Kaplan–Meier estimates (±s.e.) of annual (2002–2007), winter (2002–2008) and summer (2002–2007) survival of the Northern bobwhite in south Florida, for each management zone and zones A, B, C, D combined with (ABCDF) and without F (ABCD)

The last three rows indicate the results from the Chi-square tests for a zone effect (degrees of freedom are in parentheses). When the overall test was not significant, no *post hoc* tests were conducted (NT)

	Annual	Winter	Summer
Zones			
A	0.106 ± 0.014	0.366 ± 0.033	0.318 ± 0.027
B	0.078 ± 0.013	0.271 ± 0.031	0.295 ± 0.031
C	0.080 ± 0.012	0.317 ± 0.032	0.309 ± 0.027
D	0.103 ± 0.015	0.316 ± 0.033	0.340 ± 0.030
F	0.111 ± 0.016	0.414 ± 0.035	0.290 ± 0.030
ABCD	0.091 ± 0.007	0.319 ± 0.016	0.313 ± 0.014
Tests			
Among ABCDF	$\chi^2(4) = 5.077, P = 0.280$	$\chi^2(4) = 10.87, P = 0.028$	$\chi^2(4) = 1.763, P = 0.779$
Among ABCD	NT	$\chi^2(3) = 4.404, P = 0.221$	NT
ABCD v. F	NT	$\chi^2(1) = 6.090, P = 0.014$	NT

Table 2. Results evaluating the effect of age, sex and years on annual, winter and summer survival of northern bobwhites, during 2002–2008, on Babcock–Webb (BW) Wildlife Management Area, south Florida

AIC is the Akaike’s Information Criterion, ΔAIC the difference in AIC between the best model and the others, w_i the AIC weight of each model compared with the others and K the number of parameters. The most parsimonious models are in bold type. Effects may be additive (+) or interactive (*). Age stands for age class (juveniles versus adults)

Model	Annual survival				Winter survival				Summer survival			
	AIC	ΔAIC	w_i	K	AIC	ΔAIC	w_i	d.f.	AIC	ΔAIC	w_i	d.f.
1 Constant	18708.97	26.45	0	1	9116.84	9.80	0.003	1	10754.86	65.18	0	1
2 Age	18691.96	9.44	0.005	2	9117.37	10.33	0.002	2	10713.61	23.93	0	2
3 Sex	18710.48	27.96	0	2	9116.86	9.81	0.003	2	10752.42	62.74	0	2
4 Year	18701.16	18.64	0.000	6	9107.04	0	0.379	7	10735.94	46.26	0	6
5 Age+Sex	18693.95	11.43	0.002	3	9116.76	9.72	0.003	3	10713.99	24.31	0	3
6 Age*Sex	18691.62	9.1	0.005	4	9118.57	11.53	0.001	4	10714.31	24.63	0	4
7 Age+Year	18682.72	0.2	0.469	7	9108.03	0.99	0.232	8	10703.43	13.75	0.001	7
8 Age*Year	18682.52	0	0.519	12	9117.92	10.88	0.002	14	10689.68	0	0.999	12
9 Sex+Year	18702.31	19.79	0	7	9107.16	0.12	0.358	8	10732.54	42.86	0	7
10 Sex*Year	18709.96	27.44	0	12	9113.16	6.12	0.018	14	10739.66	49.98	0	12

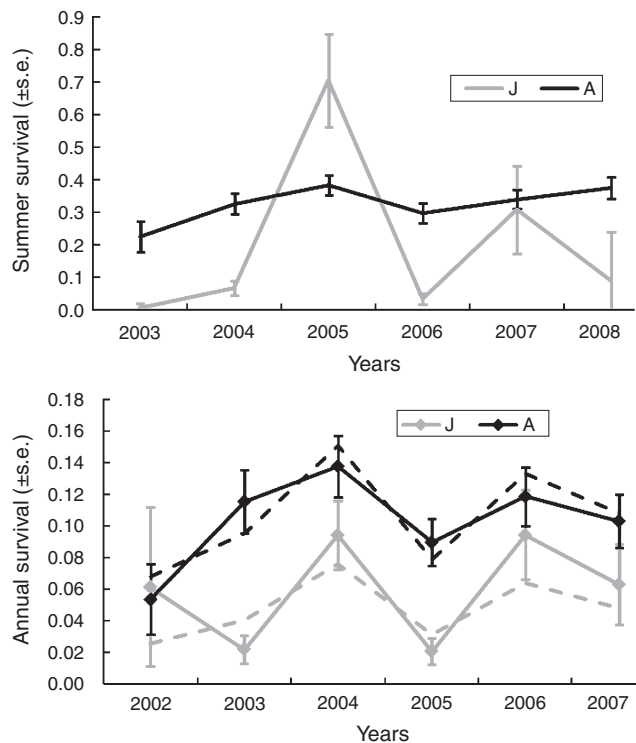


Fig. 3. Annual and summer (April–September) survival for juvenile (J) and adult (A) bobwhites in Babcock–Webb (BW) Wildlife Management Area, south Florida, USA, estimated from the model with additive effect of age class and years (dashed line) or interaction effect (solid line). Error bars indicate ±s.e.

winter survival (0.295 ± 0.014) for the 2002–2007 period. However, when data for 2008 were included in the winter analysis, winter survival increased (0.319 ± 0.014).

Winter survival

Winter survival was significantly higher in management zone F than in the other zones (zone F: 0.414 ± 0.035 , all other zones

combined: 0.319 ± 0.016 ; $\chi^2(1) = 6.090, P = 0.014$, Table 1). The three best models all included a year effect, but we did not find convincing evidence of an effect of sex or age class (models 4, 7 and 9, Table 2). We thus used the model including year effect only as a base model (model 4) for further analyses. However, when data from 2008 were removed from the analysis, this year effect was no longer detected ($AIC_{Constant} = 7954.55$ versus $AIC_{Years} = 7960.96$, Fig. 2), suggesting that winter survival remained fairly constant among years except in 2008 where survival was the highest (0.475 ± 0.042) and concomitantly, hunting effort the lowest.

There was no evidence that FSD affected winter survival. Hunting effort had a strong negative effect on survival (risk ratio = 75.95; Table 3). The most parsimonious model included the interaction between hunting effort and year, suggesting that the effect of hunting pressure on survival varied among years (model 5, Table 3). Similarly to annual survival, winter survival of birds in management zone F was the least affected by hunting effort whereas that of birds in management zone C was the lowest (Fig. 4).

Summer survival

Summer survival did not differ significantly between sexes or among management zones ($\chi^2(4) = 1.763, P = 0.779$, Table 1). The best supported model indicated a year effect in interaction with age class (model 8 in Table 2), suggesting that survival difference between age classes varied across years. Juveniles had a lower and more variable summer survival than adults (Fig. 3). Based on the best model, we then tested for additive and interactive effect of FSD, but there was no evidence that FSD influenced summer survival (Table 3).

Cause-specific mortalities

Harvesting and natural causes of mortality accounted for 36.4% and 63.6%, respectively, of total annual mortality, and for 47.1% and 52.9% of total winter mortality. Among the known causes of natural mortality, raptor and mammal predation contributed the most to both winter (47.9% and 48.7%, respectively) and summer (50.9% and 45.6%, respectively) mortalities. Mortalities from

Table 3. Results evaluating the effect of food strip densities (FSD) and hunting effort (HE) on annual, winter and summer survival of northern bobwhites, during 2002–2008, on the Babcock–Webb (BW) Wildlife Management Area, south Florida

BM is the best initial model based on selection in Table 2: Age + Years, Years and Age * Years for annual, winter and summer survivals, respectively. ΔAIC is the difference between the best model and the others, w_i the AIC weight of each model compared with the others and K the number of parameters. Effects may be additive (+) or interactive (*). Interaction terms include main effects

Model	Annual survival				Winter survival				Summer survival			
	AIC	ΔAIC	w_i	K	AIC	ΔAIC	w_i	K	AIC	ΔAIC	w_i	K
<i>FSD effect</i>												
1 BM	18682.72	0	0.602	7	9107.04	0	0.668	7	10689.68	0.05	0.402	12
2 BM+FSD	18684.59	1.87	0.236	8	9108.45	1.41	0.330	8	10691.23	1.6	0.185	13
3 BM+FSD * Years	18685.34	2.62	0.162	13	9119.42	12.38	0.001	14	10689.63	0	0.412	18
<i>Hunting effort effect^A</i>												
1 BM	18682.72	132.6	0	7	9107.04	120.9	0	7	10689.68	0	–	12
4 BM+HE	18555.32	5.23	0.059	8	8986.49	20.6	0	8	–	–	–	–
5 BM+HE * Years	18550.09	0	0.813	13	8965.89	0	1	14	–	–	–	–
6 BM+Age*HE	18553.79	3.7	0.128	9	–	–	–	–	–	–	–	–

^ANote that hunting did not occur during the summer season.

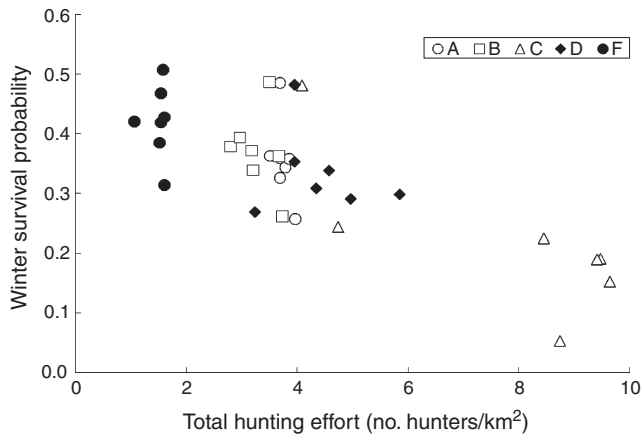


Fig. 4. Winter (October–March) survival of bobwhites on Babcock–Webb (BW) Wildlife Management Area, south Florida, USA modelled as a function of hunting effort (number of hunters per km²). The best model with an interactive effect of years and hunting effort was used. Hunting on the BW area occurred only during the winter season. For each zone (represented by a different symbol), seven estimates of survival are given corresponding to the seven winters of the study period. Highest winter survival was recorded in 2008 for every zone.

raptor and mammal predation were similar regardless of the season ($\chi^2 < 1.102$, $P > 0.294$).

Harvesting contributed to 40.3% of annual mortality in the heavily harvested zones (A, B, C and D) whereas only 8.4% of annual mortality was caused by harvest in zone F, where hunting was limited. Main known natural causes of mortality were raptor and mammal predation in all zones and seasons (Fig. 5). Raptor predation in the summer season caused a higher mortality in management zone F compared with that in all other management zones combined ($\chi^2 = 7.73$, $P = 0.005$), whereas mammal predation accounted for a similar mortality proportion in zones F and ABCD ($\chi^2 = 1.01$, $P = 0.315$). In the winter season, mortalities due to predation by raptors ($\chi^2 = 2.50$, $P = 0.114$) and mammals ($\chi^2 = 3.22$, $P = 0.073$) were similar in zone F and zones ABCD.

During summer, survival was lower for juveniles than for adults. In order to determine the cause of a higher mortality rate in juveniles, we used the best Cox proportional hazard model for summer survival with the interaction between age class and years (model 8 in Table 2) but stratified by cause of mortality. This stratified model indicated that cause-specific mortalities were similar for juveniles and adults ($F = 13.1$, d.f. = 11, $P = 0.284$). However, although not significant, mortality from all causes (except raptor predation) was higher for juveniles than for adults (Table 4).

Discussion

Development or implementation of management plans for conservation of declining populations requires knowing causes of population declines, and understanding factors affecting demographic parameters. Although habitat change is often the main cause, overharvest may also contribute to population declines in game species; however, survival has seldom been modelled as a direct function of hunting effort. Thus, our goal was

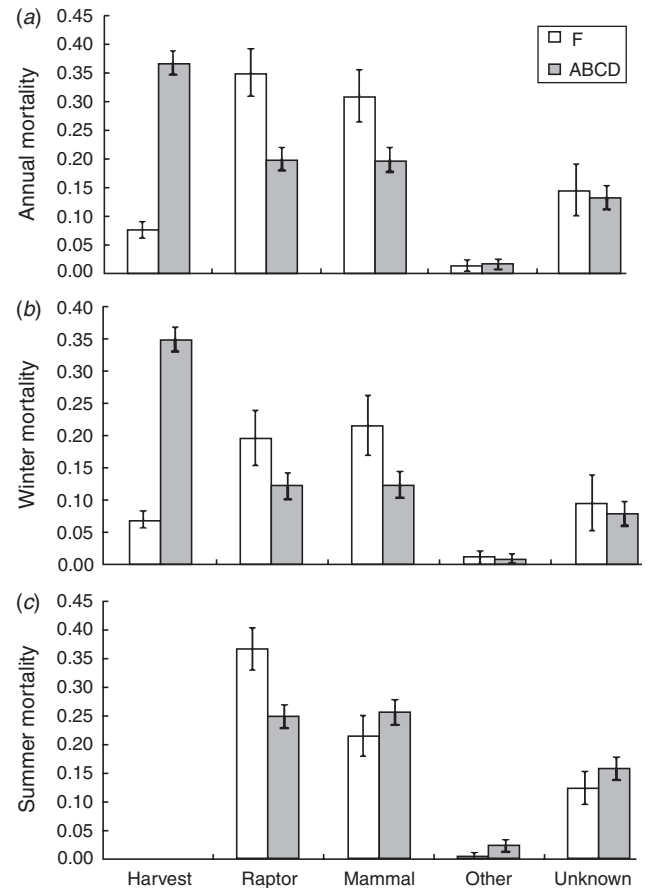


Fig. 5. Cause-specific mortality rates of bobwhites in Babcock–Webb (BW) Wildlife Management Area, south Florida, USA. These are given for field trial (zone F) versus other management zones combined (ABCD) on the (a) annual, (b) winter and (c) time summer scale. Causes of mortality were harvesting, raptor or mammal predation, ‘other’ (including snake predation) and unknown.

Table 4. Cause-specific mortality rates (\pm s.e.) for adults and juveniles during the summer season

Cause	Juveniles	Adults
Raptor	0.219 \pm 0.070	0.269 \pm 0.020
Mammal	0.340 \pm 0.112	0.237 \pm 0.020
Other	0.025 \pm 0.030	0.018 \pm 0.010
Unknown	0.164 \pm 0.047	0.137 \pm 0.018

to provide rigorous estimates of age- and sex-specific survival and to explicitly evaluate the role of hunting as a potential cause of the observed decline of bobwhite populations on the heavily hunted BW area.

Annual survival

Annual survival of bobwhites varies substantially regionally, from 0.053 in Missouri (Burger *et al.* 1995) to 0.278 in Alabama (Folk *et al.* 2007), with our estimate in the BW area positioned at the ‘low’ end of this gradient. Although males survived better than females in north Florida (Pollock *et al.*

1989a; Palmer and Wellendorf 2007; Terhune *et al.* 2007), there was no evidence that survival differed between sexes in our study population in south Florida. Our results are consistent with those reported for other bobwhite populations (Curtis *et al.* 1988; Cox *et al.* 2004) and other game species such as the willow grouse, *Lagopus lagopus* (Smith and Willebrand 1999; Robinson *et al.* 2009). Although several studies have documented similar survival for adults and juveniles (Burger *et al.* 1995; Cox *et al.* 2004; Terhune *et al.* 2007), possibly resulting from bobwhite sociality (Terhune *et al.* 2007), survival of juveniles in the BW area was lower than that of adults, a pattern also reported in other game bird species (Smith and Willebrand 1999; Duriez *et al.* 2005; Robinson *et al.* 2009).

Winter survival

Winter survival was relatively constant over the study period, and among the lowest reported (Curtis *et al.* 1988; Burger *et al.* 1998; Cox *et al.* 2004), except in 2008 after hunting regulations had been changed. Indeed, a quota of hunter days had been set, lowering the number of hunter days from a mean of 1135 to 876 and 848 in 2007 and 2008, respectively. Winter survival did not differ between sexes or age classes, most likely because males and females winter together (Smith and Willebrand 1999). Bobwhite coveys include individual of both sexes and all ages (Rosene 1969); consequently, all covey members are exposed to the same risk of mortality from predation and harvesting. In addition, when coveys are flushed during hunting activities, all birds fly off and hunters do not preferentially shoot birds of a specific age class, as evidenced by no survival effect of interaction between hunting effort and age.

Summer survival

Summer survival was also low compared with estimates reported from other studies (see Sandercock *et al.* 2008 for a review), and highly variable. There was no evidence of a sex effect on summer survival. The costs incurred by males displaying courtships or defending their territories, making them vulnerable to predation, may have been similar to the costs incurred by females producing, laying and incubating eggs and rearing a brood, as hypothesised by Burger *et al.* (1995). In addition, bobwhites have a rapid multiple clutch mating system, where males may also care for a clutch from incubation to chick independence (Curtis *et al.* 1988; Burger *et al.* 1995), thus incurring some of the same costs as females. In our study site, juveniles had a lower summer survival than adults. Mortality due to mammal predation during summer, although not significantly different, was higher for juveniles than for adults. This suggests that juveniles, being less experienced and not yet fully developed, were more vulnerable to predation and other mortality factors.

Effect of food strips

Food may be a limiting factor for game birds, especially in winter when insects are scarcer. Food limitation has been reported for bobwhites (Rosene 1969). In the BW area, we found no evidence that food strips influenced bobwhite survival in any season; these results are consistent with previous findings that food supplementation (food plots/strips or feeders) does not improve bobwhite survival (DeMaso *et al.* 1998; Guthery

et al. 2004). However, this must be interpreted with caution because the removal of these food strips could have detrimental effects. Bobwhites in our study site preferred to place home ranges and nest sites closer to food strips than expected by chance alone. Furthermore, home ranges intersecting food strips were smaller than home ranges that did not intersect food strips (Singh *et al.* in press). Thus, food strips might help enhance the quality of bobwhite habitat in the BW area.

Effect of hunting pressure

Three lines of evidence suggested that hunting substantially reduced survival of bobwhites in our study site. First, although predation was the primary cause of mortality as in other bobwhite populations (DeMaso *et al.* 1998; Rollins and Carroll 2001; Cox *et al.* 2004), hunting accounted for 47.1% and 36.4% of winter and annual mortality, respectively, in our study population; these values are higher than those reported from other bobwhite populations (Curtis *et al.* 1988; Burger *et al.* 1995). Second, winter survival of bobwhites in the field trial (zone F), where hunting is allowed only for 2 days per season, was substantially higher than in other zones where hunting pressure was higher. Finally, when survival rate was modelled as a function of hunting effort (a time-varying continuous covariate), we found that hunting effort negatively influenced bobwhite survival (Fig. 4). Differences in survival among management zones with different levels of hunting pressure might have been caused by factors other than hunting pressure, such as habitat quality or the presence of food strips. However, qualitative concurrence of all three analytical approaches leaves little doubt that hunting has a strong negative impact on bobwhite survival in the BW area. Although food strip density differed between the field trial and the other management zones, there was no evidence that food strips influenced survival. Thus, the higher winter survival in zone F compared with other zones was most likely due to a lower total hunting effort. Finally, predation caused similar mortality in all zones. This suggests that winter mortality due to harvest was probably additive (or only partially compensatory) to natural mortality, which has been reported for other bobwhite populations (Williams *et al.* 2004).

Understanding whether and to what extent hunting mortality is additive to natural mortality is important for management of harvested populations, but this has been difficult to determine (Small *et al.* 1991; Smith and Willebrand 1999; Pedersen *et al.* 2004; Duriez *et al.* 2005; Devers *et al.* 2007), partly because additivity of hunting-related mortality may vary seasonally (Jonzen and Lundberg 1999). Indeed, the difference in bobwhite winter survival between zone F and the other zones disappears on an annual scale, and summer mortality caused by raptor predation was higher in zone F than in the more heavily harvested zones, suggesting the possibility of partial compensation via predation during summer. During winter, hunting mortality was most likely additive, especially when hunting effort was high. However, there were indications of some degree of compensation at low levels of hunting (4 hunters per km²; Fig. 4). Analysis of harvest (phenomenological and mechanistic) models can help elucidate more accurately whether and to what extent hunting mortality is additive (Runge and Johnson 2002), but we lacked data for such

analyses. In the BW area, hunting effort had a variable impact on survival among years, suggesting a potentially variable role of hunting mortality. In North American mallards, hunting mortality was initially compensatory, but it progressively became totally additive (Pöysä *et al.* 2004). Seemingly compensatory role of harvest mortality can become additive over time, and this must be taken into consideration while making harvest management decisions. Compensatory mechanisms may also operate through increased reproductive effort but this seems unlikely in hunted population of tetraonids (Ellison 1991).

Synthesis and applications

Managing harvested populations that are declining is a challenging task. Wildlife managers generally are under pressure from hunters to increase or maintain hunting pressure. However, excessive hunting would not only reduce a population's capacity to produce harvestable surplus but also reduce viability of the population, especially if hunting mortality is additive to background natural mortality. Thus, a science-based approach to harvest management is needed to ensure a sustainable harvest and the long-term persistence of the population. For the bobwhite population in the BW area, we suggest that additive winter mortality due to hunting may have contributed to observed decline in our study population by reducing the number of potential breeders the following spring and thus the recruitment rate. Brennan (1991) pointed out the possibility that hunting could cause bobwhite population declines in public lands because excessive hunting may reduce recruitment of juveniles into the breeding population. In the BW area, a preliminary analysis indicated that 12.65 fledged young *per capita* would be required for the population growth rate to be stable, which is ~7-fold greater than a preliminary estimate for our study site. Thus, under present circumstances, the population cannot recover from declines because fewer and fewer individuals are recruited to the breeding pool. An accurate determination of the population-level impact of hunting may require an experimental reduction (e.g. below 4 hunters per km²) or cessation of hunting in all zones for some years, and evaluating population's response. Such an experimental approach within the framework of adaptive management would be helpful in developing harvest management strategies, and would also contribute to recovery efforts.

Our study provides evidence that harvest has contributed to bobwhite population decline in our study site. Although the habitat is intensively managed in our study site, we cannot rule out the possible role of habitat quality because the efficacy of habitat management activities has not been thoroughly evaluated. A comprehensive approach that incorporates harvest management and habitat improvements is needed to ensure the long-term persistence of the bobwhite population in the BW area. Improving escape cover could help reduce predation-related mortality, the most important cause of mortality during summer (Williams *et al.* 2000). Although food strips did not seem to influence survival directly, they affect home-range size and habitat (including nest site) selection by bobwhites in the BW area (Singh *et al.* in press). Thus, habitat management practices aimed at providing compositionally and structurally diverse habitat that can provide a diversity of food and cover

resources throughout the year would likely benefit bobwhite population in our study site.

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