

Journal of Applied Ecology

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Journal:	<i>Journal of Applied Ecology</i>
Manuscript ID:	Draft
Manuscript Type:	Standard Paper
Date Submitted by the Author:	
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Key-words:	Northern bobwhite quail, <i>Colinus virginianus</i> , hunting effort, survival modeling, cause-specific morality, population decline, wildlife harvest

1 IMPACT OF HARVEST ON SURVIVAL OF A HEAVILY HUNTED
2 GAME BIRD POPULATION
3

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13 Running title: Harvest and Northern bobwhite survival

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15 Word count: 7,793

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Summary

1. Despite their economic importance and intensive management, many game bird species including the Northern bobwhite 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. Thus, the aims of this study were 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.
2. 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 we used the nonparametric cumulative incidence function estimator to estimate cause-specific mortality rates.
3. Mean annual survival (0.091 ± 0.006) on BW area was lower than most estimates reported for other bobwhite populations. Annual survival differed between age classes 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. Hunting effort had a substantial negative impact on survival in all management zones. In the lightly-hunted field trial, winter 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

1 bobwhite mortality during summer was mainly due to raptor (39.7%) and mammalian
2 predation (35.6%), whereas that during winter was primarily caused by hunting (47.1%).

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

7 5. *Synthesis and applications.* Our results suggest that reduction in hunting pressure may be
8 necessary to reverse the declining population trends in heavily hunted game species in
9 public lands, such as the Northern bobwhites in BW area.

10
11 Keywords: Northern bobwhite quail, *Colinus virginianus*, hunting effort, survival modeling, cause-
12 specific mortality, population decline, wildlife harvest

15 Introduction

16
17 The Northern bobwhite quail *Colinus virginianus* (hereafter bobwhites), one of the most
18 economically important game species in the southeastern United States (Burger et al. 1999), has
19 declined dramatically throughout most of its range (Sauer et al. 2008), primarily because of
20 habitat loss and fragmentation (Dimmick et al. 2002). In public lands, hunting pressure is
21 intense. In the Babcock-Webb Wildlife Management Area (BW area), a large but isolated state-
22 owned land in southwest Florida, USA, annual harvest records suggest that the bobwhite

1 population has substantially declined since 1980's. Prior to 1980, annual harvests frequently
2 exceeded 4000 quails, with >9000 birds harvested in 1976. Harvest declined substantially
3 thereafter, with only 846 quails harvested in 2001 (Dimmick et al. in press; Florida Fish and
4 Wildlife Conservation Commission, unpublished data). The habitat has been intensively
5 managed for bobwhites using widely-used management techniques, including roller-chopping,
6 prescribed fires and food strips (long, narrow food plots). This raises the possibility that
7 overharvest caused, or contributed to, observed population declines; this possibility, however,
8 has not been thoroughly assessed.

9 Several studies have evaluated impact of hunting on game birds either by comparing
10 cause-specific mortalities (Burger et al. 1995; Alonso et al. 2005; Robinson et al. 2009) or by
11 experimentally testing for the difference in survival (Smith and Willebrand 1999; Devers et al.
12 2007) or abundance (Connelly et al. 2003; Pedersen et al. 2004; Thiollay 2005) between
13 management zones with different levels of hunting pressure. Few studies have attempted to
14 directly test for the relationship between hunting effort and survival or abundance (Vangilder and
15 Kurzejeski 1995; De Leo et al. 2004). Another challenging issue in management of harvested
16 populations is to determine whether mortality due to exploitation is additive to natural mortality,
17 or is partially/totally compensatory. If hunting mortality is compensatory, managers may need to
18 know the threshold of harvest rate above which the population would be adversely affected. A
19 direct evaluation of the relationship between survival or abundance and hunting effort may help
20 determine this threshold.

21 Mortality rates may vary annually and/or seasonally, and be influenced by several
22 intrinsic factors such as age and sex, and extrinsic factors such as food resources and
23 management actions. In short-lived bird species, adult survival is expected to have a higher

1 annual variability than reproductive parameters (Saether and Bakke 2000). Furthermore, game
2 birds may be exposed to different mortality factors throughout the year. Hunting generally occurs
3 during a limited period in winter, while predation risk may be higher during the breeding season.
4 Predation risk may differ between sexes. Indeed, risk of predation may be a cost of reproduction
5 for more conspicuous and/or less vigilant males while displaying courtship, competing for
6 females or defending their territories, and for more vulnerable females while on the nest during
7 laying and incubation periods and while providing parental care (Magnhagen 1991). Also,
8 juveniles, being smaller, underdeveloped and inexperienced are likely to experience a higher
9 mortality than adults (Roff 1992).

10 Understanding the relative influence of quality habitat and hunting pressure on
11 demographic parameters and population dynamics is crucial for effective management of game
12 species. First, the impact of hunting pressure on season-, age- and sex-specific survival must be
13 determined. Also, current management actions such as food supplementation (e.g., feeders or
14 food plots) and predator control should be evaluated since they may be inefficient or have
15 unexpected negative effects (Bro et al. 2004; Evans 2004). A second step would be to integrate
16 these relationships into a population model to assess the population-level impact of hunting
17 pressure, and evaluate what level of hunting effort/harvest rate, if any, would be sustainable.

18 In this study, we focused on evaluating the direct impact of hunting effort on bobwhite
19 survival in the BW area. We intensively monitored radio-tagged bobwhites for 6 years, and used
20 these data to (1) estimate survival probabilities, (2) test for annual and seasonal variation, and
21 sex- and age-specific differences in survival probabilities, (3) assess the effect of hunting
22 pressure on bobwhite survival, and (4) quantify annual and seasonal cause-specific mortality
23 rates.

1

2 Material and methods

3 Study species and sites

4 Northern bobwhite quails are small (140-170g) and short-lived (average <1 year) land birds
5 (Brennan 1999). The breeding season starts in late winter with courtship displays. Clutches of
6 12 eggs on average (range 5-18) are incubated for 23 days, and the first peak of hatching occurs
7 between late May and mid-June. Renesting is common. During fall and winter, adults and
8 juveniles of both sexes gather in coveys (group of usually 12-15 individuals) to overwinter.
9 Hunting generally occurs during this period. Bobwhites are exposed to predation throughout the
10 year, and common predators include raptors (several species of hawks and owls), mammals (e.g.,
11 grey fox *Urocyon cinereoargenteus*, raccoons *Procyon lotor*, bobcats *Lynx rufus*, coyotes *Canis*
12 *latrans*) and snakes.

13 The study was conducted on the Babcock-Webb Wildlife Management Area (26,799 ha),
14 Charlotte County, in southwest Florida (Fig.1). The most significant plant communities included
15 dry prairie, pine-palmetto and wet prairie (A. Singh, unpublished data). The area is subject to
16 periodic short-duration flooding and prolonged drought. Prescribed burning, roller-chopping and
17 *Sesbania sp.* food strips (composing 0.56% of the total area) are currently the primary habitat
18 management activities. The BW area is divided into five management zones A (6,342 ha), B
19 (6,258 ha), C (5,396 ha), D (5,689 ha), and a field trial course F (3,132 ha; Fig.1). The spatial
20 density of food strips, constant over the study period, was 30.81, 39.77, 49.22, 52.25 and 161.24
21 m²/ha in zones A, B, C, D and F respectively. The first four zones (A, B, C and D) are open to
22 hunting from mid-November to late December whereas in the field trial area (F), hunting is

1 permitted only for two days in late January (for a maximum of 25 hunters each day). The daily
2 bag limit was set at 6 quail per hunter for every zone. However, zones A and B were designated
3 as limited access (10 hunters per day) whereas access to zones C and D was unlimited, with zone
4 C by far preferred by hunters.

5

6 Field methods

7 Birds were captured between October 2002 and March 2009 with baited funnel traps. Birds were
8 weighed to the nearest gram, aged, sexed, and leg-banded. Birds weighing at least 130 g were
9 radio-marked with a 6-g necklace-style transmitter with a mortality sensor (American Wildlife
10 Enterprises, B. Mueller, Monticello, USA). Antenna length was 22 cm. Transmitters had an
11 expected battery life of 365 days and a signal range of about 500 to 1000 m in the BW area.
12 Individual bird locations were attempted at 3-5 day intervals. Radioed birds were located using
13 hand-held receivers and Yagi antennas. Cast nets approximately 3 m in diameter were used to
14 capture unmarked birds that were associated with radio-tagged birds. Bird dogs helped to locate
15 new birds not associated with radio-tagged birds. Birds missing for several days were located
16 with a truck-mounted whip antenna. When a mortality signal was received, the bird was
17 immediately located and probable cause of death determined. During the hunting season, we
18 searched for unrecovered injured or dead radio-marked birds every 2 days. All trapping and
19 handling protocols were approved by the University of Florida Institutional Animal Care and
20 Use Committee (protocol number A-794).

21

22 Survival analysis

1 A total of 2066 radio-tagged individuals was used in the survival analyses. Sex ratio was biased
2 towards males (745 females and 1321 males). However, this bias was mainly recorded for adults
3 (sex ratio of females to males of 0.48) and not for juveniles (sex ratio of 0.93). We used Cox's
4 proportional hazard models with the *coxph* procedure implemented in the *survival* package of the
5 R software (R Development Core Team 2008). Tied failure times were handled with the "Efron"
6 method and we chose the Kaplan-Meier option for the baseline function (Therneau and
7 Grambsch 2000).

8 We analyzed annual survival (i.e., survival from the 1st of October of year t to the 30th of
9 September of year $t+1$) by using the following stepwise approach. We first tested for the effect
10 of age (juveniles: birds hatched in summer of year t ; and adults: birds hatched all previous
11 years), sex (males and females) and year as survival can differ between sexes and vary
12 seasonally as well as annually (e.g., Terhune et al. 2007). We also tested for additive and
13 interactive effects of these three covariates. Model comparison was performed with the Akaike's
14 Information Criterion (AIC). When the difference in AIC value exceeded two, the best model
15 was the model with the lowest AIC. Otherwise, models were assumed to be not different and we
16 selected the most parsimonious model, i.e., the model with the lowest number of parameters
17 (Burnham and Anderson 2002).

18 Next, we used the most parsimonious model from the preceding analyses for the
19 following two sets of analyses. In the first set, we tested for the additive and interactive effects of
20 *Sesbania* food strip density (FSD). In the second set, we tested for the effect of hunting pressure
21 in two ways. First, we tested for the "Zone" effect (A, B, C, D and F; see "study species and
22 sites" for details). Secondly, since Cox's models estimate daily survival, we modeled survival as
23 a direct function of hunting effort defined as the number of hunters per day and km² in each zone

1 for each hunting season (i.e., around 40 days in zones A, B, C, D and 2 days in the field trial).
2 Although total hunting effort over the winter was the lowest in zone F, hunting effort per day
3 there was the highest among all zones in all years (Fig.2). Note that hunting effort was highly
4 correlated with harvest effort, i.e., number of quails harvested per day and km² ($r^2 = 0.867$, $P <$
5 0.001).

6
7 In addition to annual survival, we also analyzed seasonal survival because mortality
8 factors may vary seasonally and also because hunting occurred only from November to January.
9 We considered the period from the 1st of October to the 31st of March as *winter season*, and the
10 period from the 1st of April to the 30th of September as *summer season*. Because survival
11 estimates were based on different (summer and winter) datasets, an AIC-based approach was
12 inappropriate. Thus, to test for a difference in survival between summer and winter seasons, we
13 used program CONTRAST which allows comparison of multiple survival estimates (Hines and
14 Sauer 1989). Then, we analyzed summer and winter survivals separately, following the same
15 approach as previously described for annual survival, but without tests for the effect of hunting
16 on summer survival.

17 Statistical inferences in all analyses were based on an information-theoretic approach
18 (using the AIC and the AIC weights) with one exception. Proportional hazard assumption was
19 tested for categorical covariates, using the R procedure *cox.zph*, which tests for linear changes in
20 the effects of covariates on hazard over time (Therneau and Grambsch 2000). We did not find
21 violation of this assumption, except for the zone effect. This is not surprising since harvest
22 happened at different times and different lengths of time in the different zones. We thus

1 estimated annual, winter and summer survival for each zone with the Kaplan-Meier staggered-
2 entry method (Pollock et al. 1989b) using the procedure *survfit* also available in the R *survival*
3 package and then used CONTRAST software to test for an overall zone effect on these estimates
4 and to perform post-hoc tests when the overall was significant.

5

6 Cause-specific mortality

7 Each known mortality event was attributed to one of five causes: (1) harvest, (2) predation by
8 raptors, (3) predation by mammalian predators, (4) other causes including predation by snakes,
9 and (5) unknown. Cause-specific mortality rates were estimated using the non-parametric
10 cumulative incidence function estimator. This is a generalization of the Kaplan-Meier staggered-
11 entry method that uses information on the number and timing of deaths from each cause and the
12 number of radio-tagged individuals at risk (Heisey and Patterson 2006). Because the proportional
13 hazard assumption was not met with the management zone as a covariate, we could not use the
14 stratified Cox proportional hazard models to test for difference in cause-specific mortality rates
15 between management zones A, B, C and D and zone F. We thus used the CONTRAST software
16 to compare cause-specific mortality rates among management zones.

17

18 Results

19

20 Annual survival

1 Average annual survival was 0.091 ± 0.006 between 2002 and 2007 and varied among years
2 (Fig.3). Annual survival was not significantly different among zones (Table 1). The two highest
3 ranked models indicated that annual survival varied with age and among years with no
4 convincing evidence of a sex effect (models 7 and 8, Table 2). We chose the model with the
5 additive effect of age and years (model 7, Table 2) for further analysis because this model had
6 fewer parameters, and also because survival of adults and juveniles varied similarly during the
7 study period (Fig. 4). Overall, adults had a higher mean annual survival than juveniles ($0.111 \pm$
8 0.008 and 0.052 ± 0.008 , respectively).

9 Using the model with an additive effect of age and year as the base model, we tested for
10 the effects of food strip density (FSD) and hunting effort. There was no evidence that FSD
11 influenced annual survival; the addition of the FSD covariate did not improve the parsimony of
12 the base model (Table 3). On the other hand, there was strong evidence that hunting effort
13 substantially negatively affected annual survival (risk ratio: 26.01) but its influence varied
14 among years; including an interaction between years and hunting effort resulted in a far better
15 model in terms of AIC (model 5, Table 3). Survival of birds in the management zone F, where
16 hunting effort was the lowest, was the least affected by hunting effort. Conversely, in the
17 management zone C, where hunting effort was the highest because of higher hunter preference
18 permitted by easier access, exhibited the lowest survival. Survival of birds in the management
19 zones A, B and D was intermediate.

20 Finally, there was no evidence for an interaction effect of hunting effort and food strip
21 density (model 7, Table 3).

22

1 Seasonal variation

2 Summer survival (0.307 ± 0.013), although slightly higher, did not significantly differ ($\chi^2 =$
3 0.391 , $df = 1$, $P = 0.532$) from winter survival (0.295 ± 0.014) for the 2002-2007 period.
4 However, when data for 2008 were included in the analysis, winter survival substantially
5 increased (0.319 ± 0.014).

6

7 Winter survival

8 Winter survival was significantly higher in management zone F than in the other zones (zone F:
9 0.414 ± 0.035 , all other zones combined: 0.319 ± 0.016 ; Table 1). The three best models all
10 included a year effect, but we did not find convincing evidence of an effect of sex or age (models
11 4, 7 and 9, Table 2). We thus used the model including year effect only as a base model (model
12 4) for further analyses. However, when data from 2008 were removed from the analysis, this
13 year effect was no longer detected ($AIC_{\text{Constant}} = 7954.55$ vs. $AIC_{\text{Years}} = 7960.96$, Fig. 3),
14 suggesting that winter survival remained fairly constant among years except in 2008 where
15 survival was the highest (0.475 ± 0.042) and concomitantly, hunting effort the lowest.

16 There was no evidence that food strip density affected winter survival. Hunting effort had
17 a strong negative effect on survival (risk ratio = 75.95; Table 3). The most parsimonious model
18 included the interaction between hunting effort and year, suggesting that the effect of hunting
19 pressure on survival varied among years (model 5, Table 3). When testing for the interaction
20 effect of food strip density and hunting effort, the model with this additional covariate (model 7,
21 Table 3) was the best in terms of AIC. Hunting effort strongly increased mortality risk (risk ratio
22 = 260.92, $Z = 3.810$, $P < 0.001$) whereas food strip density had no impact (risk ratio = 1.001, $Z =$

1 0.698, $P = 0.49$) in itself. However, although food strip density tended to compensate for the
2 negative effect of hunting effort, this interaction effect was not significant (risk ratio = 0.978, $Z =$
3 -1.926 , $P = 0.054$). The difference in AIC being ≤ 2 with the second best model (Table 3), we
4 retained the most parsimonious model without the interaction term between food strip density
5 and hunting effort (model 5, Table 3). Winter survival estimated from the most parsimonious
6 model was plotted for each zone and year against total hunting effort over the winter season for
7 more clarity (Fig. 5). Similarly to annual survival, winter survival of birds in the management
8 zone F was the least affected by hunting effort whereas that of birds in the management zone C
9 was the lowest (Fig. 5).

10

11 Summer survival

12 Summer survival did not differ significantly between sexes or among management zones (Table
13 1). The best supported model indicated a year effect in interaction with age (model 8 in Table 2),
14 suggesting that survival difference between age classes varied across years. Juveniles had a
15 lower and more variable summer survival than adults (Fig. 4). Based on the best model, we then
16 tested for additive and interactive effect of food strip density, but there was no evidence that food
17 strip density influenced summer survival (Table 3).

18

19 Cause-specific mortalities

1 Harvesting was the main cause of annual mortality, followed by predation (Fig. 6). Raptor and
2 mammal predation contributed similarly to mortalities in both the winter and the summer seasons
3 ($\chi^2 < 1.102$, $P > 0.294$).

4 Cause-specific mortalities in management zones with high hunting pressure (A, B, C and
5 D) were compared with those in zone F where hunting was limited. Harvesting was by far the
6 most important cause of annual mortality in the heavily harvested zones whereas mortality in
7 zone F was mostly caused by raptor and mammal predation (Fig. 7). Raptor predation in the
8 summer season caused a higher mortality in management zone F compared to that in all other
9 management zones combined ($\chi^2 = 7.73$, $P = 0.005$), whereas mammal predation accounted for a
10 similar mortality proportion in zones F and ABCD ($\chi^2 = 1.01$, $P = 0.315$). In the winter season,
11 mortalities due to predation by raptors ($\chi^2 = 2.50$, $P = 0.114$) and mammals ($\chi^2 = 3.22$, $P = 0.073$)
12 were similar in zone F and zones ABCD.

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

20

21 Discussion

22

1 Development or implementation of management plans for conservation of threatened or
2 declining populations requires knowing causes of population declines, and understanding factors
3 affecting demographic parameters. Although changes in quantity and quality of habitat are often
4 the main cause, overharvest may also contribute to population declines in game species;
5 however, survival has seldom been modeled as a direct function of hunting effort. Thus, our goal
6 was to provide rigorous estimates of age- and sex-specific survival and to explicitly evaluate the
7 role of hunting as a potential cause of the observed decline of bobwhite populations on the
8 heavily hunted BW area.

9

10 Annual survival

11 Annual survival of bobwhites varies substantially regionally, from 0.053 in Missouri (Burger et
12 al. 1995) to 0.278 in Alabama (Folk et al. 2007), with our estimate in the BW area positioned at
13 the “low” end of the gradient of survival. In North Florida, males survived better than females
14 (Pollock et al. 1989a; Palmer and Wellendorf, 2007; Terhune et al. 2007). However, in our study
15 population in South Florida, there was no evidence that survival differed between males and
16 females. These results are consistent with those reported for other bobwhite populations (Curtis
17 et al. 1988; Cox et al. 2004) and other game species such as the willow grouse *Lagopus lagopus*
18 (Smith and Willebrand 1999; Robinson et al. 2009). Several studies have documented similar
19 survival for adults and juveniles (Burger et al. 1995; Cox et al. 2004; Terhune et al., 2007), and
20 bobwhite sociality has been offered as an explanation for the lack of age-specific differences in
21 survival (Terhune et al. 2007). However, on BW area, survival of juveniles was lower than that

1 of adults, a pattern also reported in other game bird species (Smith and Willebrand 1999; Duriez
2 et al. 2005; Robinson et al. 2009).

3

4 Winter survival

5 Winter survival was relatively constant over the study period, and among the lowest reported
6 (Curtis et al. 1988; Burger et al. 1998; Cox et al. 2004), except in 2008 after hunting regulations
7 had been changed. Indeed, a quota of hunter days had been set, lowering the number of hunter
8 days from a mean of 1135 to 876 and 848 in 2007 and 2008 respectively. Winter survival did not
9 differ between sexes or age classes. As hypothesized for the willow grouse, this may be because
10 males and females winter together (Smith and Willebrand 1999). Bobwhite coveys include
11 individual of both sexes and all ages (Rosene 1969); consequently, all covey members are
12 exposed to the same risk of mortality from predation and harvesting. In addition, when coveys
13 are flushed during hunting activities, all birds fly off and hunters do not seem to preferentially
14 shoot birds of a specific age class, as supported by our results indicating no interaction between
15 hunting effort and age on bobwhite survival.

16

17 Summer survival

18 Summer survival was also low compared to estimates reported in other studies (see Sandercock
19 et al. 2008 for a review). Contrary to winter survival, summer survival was highly variable and
20 this contributed to the substantial variability in estimated annual survival. We did not find any
21 evidence of a sex effect on summer survival. The costs incurred by males displaying courtships

1 or defending their territories making them at high risk of raptor predation may have been
2 balanced by the costs for females to produce, lay and incubate eggs and rear a brood as
3 hypothesized by Burger et al. (1995). In addition, the Northern bobwhite quail has a rapid
4 multiple clutch mating system, where males may also care for a clutch from incubation to chick
5 independence (Curtis et al. 1988; Burger et al. 1995). This implies that a certain proportion of
6 males may have incurred some of the same costs as females. In our study site, juveniles had a
7 lower summer survival than adults. Mortality due to mammal predation during summer, although
8 not significantly different, was higher for juveniles than for adults. This suggests that juveniles
9 were more vulnerable to predation and maybe extreme weather conditions, because they are less
10 experienced and not yet fully developed.

11

12 Effect of food strips

13 Food may be a limiting factor for game birds, especially in winter when insects are scarcer. Food
14 limitation has been reported for bobwhites (Rosene 1969). In the BW area, we found no evidence
15 that food strips influenced bobwhite survival in any season; these results are consistent with most
16 of those reported for other bobwhite populations (DeMaso et al. 1998; Guthery et al. 2004) in
17 that food supplementation (with plots/strips or feeders) did not seem to improve survival.
18 However, these results must be interpreted with caution because the removal of these food strips
19 could have detrimental effects. Bobwhites in our study site preferred to place home ranges and
20 nest sites closer to food strips than expected by chance alone. Furthermore, bobwhites whose
21 home ranges intersected food strips had smaller home ranges compared to those whose home
22 ranges did not intersect food strips (A. Singh, unpublished data). Finally, we found that density

1 of food strips partially compensated for the negative effect of hunting on bobwhite survival,
2 perhaps by providing food and/or cover during winter. Thus, despite the lack of evidence that
3 food strips improved bobwhite survival, they might help enhance the quality of bobwhite habitat
4 on the BW area.

5

6 Effect of hunting pressure

7 Three lines of evidence suggested that hunting substantially reduced survival of bobwhites in our
8 study site. First, analysis of cause-specific mortality revealed that hunting was the most
9 important mortality factor during winter as well as annually, accounting for 47.1% and 36.4% of
10 mortality, respectively. In many other bobwhite populations, predation is the most important
11 cause of mortality (Curtis et al. 1988; Burger et al. 1995, 1998; DeMaso et al. 1998; Rollins and
12 Carroll 2001; Cox et al. 2004). Secondly, winter survival of bobwhites in the field trial (zone F),
13 where hunting is allowed only for two days per season, was substantially higher than in other
14 zones where hunting pressure was much higher. Finally, when survival rate was modeled as a
15 function of hunting effort (a time-varying continuous covariate), we found that hunting effort
16 negatively influenced bobwhite survival (Fig. 5). One might argue that a zone effect (i.e.,
17 differences in survival among management zones with different levels of hunting pressure) might
18 be caused by factors other than hunting pressure; such factors may include habitat quality or the
19 presence of food strips. However, qualitative concurrence of all three analytical approaches
20 leaves little doubt that hunting has a strong negative impact on bobwhite survival, and has likely
21 contributed to observed declines in bobwhite abundance on BW area. An important difference
22 between management zones A, B, C, D, and field trial (F) was density of food strips. However,

1 no effect of food strip density on survival was detected, and the higher winter survival in zone F
2 compared to other zones was most likely due to a lower total hunting effort. The second major
3 mortality factor during winter was raptor and mammal predation, but predation caused similar
4 mortality rates in all zones. This suggests that winter mortality due to harvest was probably
5 additive (or only partially compensatory) to natural mortality, which was also reported for other
6 bobwhite populations (Pollock et al. 1989a; Williams et al. 2004).

7 Understanding whether and to what extent hunting mortality is compensatory or additive
8 to natural mortality is important for management of harvested populations, but this has been
9 difficult to determine (Small et al. 1991; Smith and Willebrand 1999; Pedersen et al. 2004;
10 Duriez et al. 2005; Devers et al. 2007), partly because additivity of hunting-related mortality may
11 vary seasonally (Jonzen and Lundberg 1999). Indeed, the difference in bobwhite winter survival
12 between zone F and the others disappears on an annual scale, and summer mortality caused by
13 raptor predation was much higher in zone F than in the more heavily harvested zones. This
14 suggests that hunting mortality may be additive during winter but with a partially compensatory
15 mechanism occurring via predation during summer. Analysis of harvest (phenomenological and
16 mechanistic) models can help elucidate whether or not hunting mortality is additive (Runge and
17 Johnson 2002), but we lacked data for such analyses. In our study population, hunting effort had
18 a variable impact on survival among years, suggesting a potentially variable role of hunting
19 mortality. In North American mallards, hunting mortality was initially compensatory, but
20 progressively evolved toward totally additivity (Poysa et al. 2004). Seemingly compensatory role
21 of harvest mortality can become additive over time, and this must be taken into consideration
22 while making harvest management decisions. Compensatory mechanisms may also operate

1 through increased reproductive effort but this seems unlikely in hunted population of tetraonids
2 (Ellison 1991).

3

4 Synthesis and applications

5 Managing harvested populations that are declining is a challenging task. Wildlife managers
6 generally are under pressure from hunters to increase or maintain hunting pressure. However,
7 excessive hunting would not only reduce a population's capacity to produce harvestable surplus
8 but also reduce viability of the population, especially if hunting mortality is additive to
9 background natural mortality. Thus, a science-based approach to harvest management is needed
10 to ensure that harvest is sustainable and that long-term persistence of the population is not
11 threatened. For the bobwhite population on the BW area, we suggest that additive winter
12 mortality due to hunting most likely contributed to observed decline in our study population.
13 Brennan (1991) pointed out the possibility that hunting could cause bobwhite population declines
14 in public lands because excessive hunting may reduce recruitment of juveniles into the breeding
15 population. On BW area, only about 5% of juveniles survive their first year to become
16 reproductive adults, which means that 17.09 new individuals per individual already in the
17 population would be required for the population growth rate to be stable. However, estimates of
18 clutch size (12.11), hatchability (0.85) and nest survival (0.42) on BW area (V. Rolland,
19 unpublished data) would produce only 4.34 new individuals per capita. Consequently, population
20 cannot recover from declines because fewer and fewer individuals are recruited to the breeding
21 pool. An accurate determination of the population-level impact of hunting may require an
22 experimental reduction of hunting in all zones or cessation of hunting for some years, and

1 evaluating population's response. Such an experimental approach within the framework of
2 adaptive management would be extremely helpful in developing harvest management strategies,
3 and would contribute to recovery efforts.

4 Our study provides evidence that overharvest has contributed substantially to bobwhite
5 population decline in our study site, but we cannot rule out the possible role of habitat
6 degradation. A comprehensive approach that incorporates hunting management and habitat
7 improvements is needed to ensure the long-term persistence of the bobwhite population on BW
8 area. Improving escape cover could help reduce predation-related mortality, the most important
9 cause of mortality during summer (Williams et al. 2000). Although food strips did not seem to
10 influence survival directly, they affect home range size and habitat (including nest site) selection
11 by bobwhites on BW area (A. Singh, unpublished data). Thus, habitat management practices
12 aimed at providing compositionally and structurally diverse habitat that can provide a diversity
13 of food and cover resources throughout the year would likely benefit bobwhite population in our
14 study site.

16 Acknowledgements

17 We thank R. Dimmick for leading field data collection efforts, and S. & A. Brinkley, G.
18 Coker, D. Caudill, D. Holt, J. McGrady, J. Sloane, and J. Scott for their significant contribution
19 to data collection. We are grateful to the many volunteers from the Southwest Florida Chapter of
20 Quail Unlimited who aided the research in many ways. We also acknowledge A. Singh for
21 preliminary data analysis, K. Pollock and R. Dorazio for statistical advice, C. McKelvy and T.
22 O'Meara for valuable advice throughout the study, and N. Hyslop and Fred Johnson for helpful

1 comments on earlier drafts. Research was funded by the Florida Fish and Wildlife Conservation
2 Commission, and the Department of Wildlife Ecology and Conservation, University of Florida.

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12

1 Table 1. Kaplan-Meier estimates (\pm SE) of annual (2002-2007), winter (2002-2008) and summer
 2 (2002-2007) survival of the Northern bobwhite in south Florida, indicated for each management
 3 zone. The last three rows indicate the results from the Chi-square tests for a zone effect (degrees
 4 of freedom are in parentheses). When the overall test was not significant, no post-hoc tests were
 5 conducted (NT).

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

17

18 Table 2. Results evaluating the effect of age, sex and years on annual, winter and summer survival of Northern bobwhites in south Florida. AIC is
 19 the Akaike's Information Criterion, Δ AIC the difference in AIC between the best model and the others, AICw the AIC weight of each model
 20 compared to the others and np the number of parameters. The most parsimonious models are in bold type. Effects may be additive (+) or
 21 interactive (*).

		Annual survival				Winter survival				Summer survival				
	Model	AIC	Δ AIC	AICw	np	AIC	Δ AIC	AICw	np	AIC	Δ AIC	AICw	np	
24	1	Constant	18708.97	26.45	0	0	9116.84	9.80	0.003	0	10754.86	65.18	0	0
25	2	Age	18691.96	9.44	0.005	1	9117.37	10.33	0.002	1	10713.61	23.93	0	1
26	3	Sex	18710.48	27.96	0	1	9116.86	9.81	0.003	1	10752.42	62.74	0	1
27	4	Year	18701.16	18.64	0.000	5	9107.04	0	0.379	6	10735.94	46.26	0	5
28	5	Age+Sex	18693.95	11.43	0.002	2	9116.76	9.72	0.003	2	10713.99	24.31	0	2
29	6	Age*Sex	18691.62	9.1	0.005	3	9118.57	11.53	0.001	3	10714.31	24.63	0	3
30	7	Age+Year	18682.72	0.2	0.469	6	9108.03	0.99	0.232	7	10703.43	13.75	0.001	6
31	8	Age*Year	18682.52	0	0.519	11	9117.92	10.88	0.002	13	10689.68	0	0.999	11

32	9	Sex+Year	18702.31	19.79	0	6	9107.16	0.12	0.358	7	10732.54	42.86	0	6
33	10	Sex*Year	18709.96	27.44	0	11	9113.16	6.12	0.018	13	10739.66	49.98	0	11

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34 Table 3. Results evaluating the effect of food strip densities (FSD) and hunting effort (HE) on annual, winter and summer survival of Northern
 35 bobwhites in south Florida. BM is the best initial model based on selection in Table 2: Age+Years, Years and Age*Years for annual, winter and
 36 summer survivals, respectively. Δ AIC is the difference between the best model and the others, AICw the AIC weight of each model compared to
 37 the others and np the number of parameters. Effects may be additive (+) or interactive (*). Main effects not clearly explicit are included in the
 38 interaction term.

		Annual survival				Winter survival				Summer survival			
Model		AIC	Δ AIC	AICw	np	AIC	Δ AIC	AICw	np	AIC	Δ AIC	AICw	np
<i>FSD effect</i>													
1	BM	18682.72	0	0.602	6	9107.04	0	0.668	6	10689.68	0.05	0.402	11
2	BM+FSD	18684.59	1.87	0.236	7	9108.45	1.41	0.330	7	10691.23	1.6	0.185	12
3	BM+FSD*Years	18685.34	2.62	0.162	12	9119.42	12.38	0.001	13	10689.63	0	0.412	17
<i>Hunting effort effect[#]</i>													
1	BM	18682.72	132.6	0	6	9107.04	120.9	0	6	10689.68	0	-	11
4	BM+HE	18555.32	5.23	0.059	7	8986.49	20.6	0	7	-	-	-	-

48	5	BM+HE*Years	18550.09	0	0.813	12	8965.89	0	1	13	-	-	-	-	-
49	6	BM+Age*HE	18553.79	3.7	0.128	8	-	-	-	-	-	-	-	-	-

50 *Interaction effect of hunting effort and FSD*

51	5	BM+HE*Years	18550.09	0	0.444	12	8965.89	0.97	0.334	13					
52	7	BM+Years*HE	18550.35	0.26	0.390	14	8964.92	0	0.543	15					
53		+HE*FSD													
54	8	BM+Years*HE	18552.07	1.98	0.165	13	8967.89	2.97	0.123	14					
55		+HE+FSD													

56 #Note that hunting did not occur during the summer season.

Table 4. Cause-specific mortality rates (\pm SE) 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	0.0184 \pm 0.010
Unknown	0.164 \pm 0.047	0.137 \pm 0.018

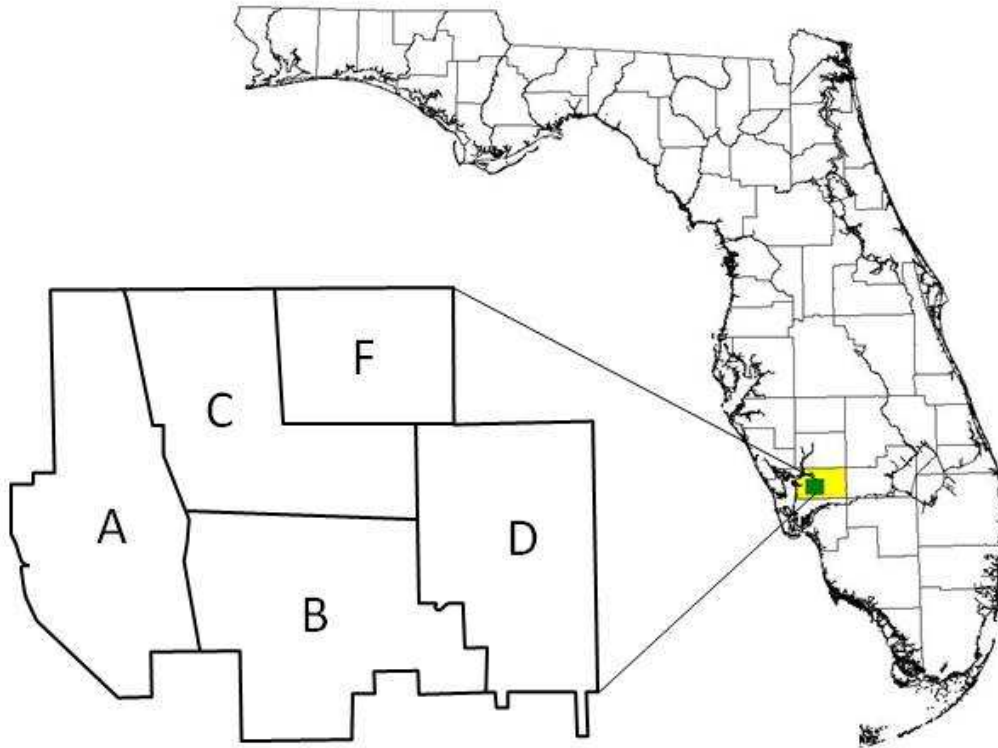


Figure 1. Location of the BW area, Charlotte County, south Florida, USA. The area is divided into five management zones (A, B, C, D and F) with different levels of hunting pressure and food strip density (see text for details).

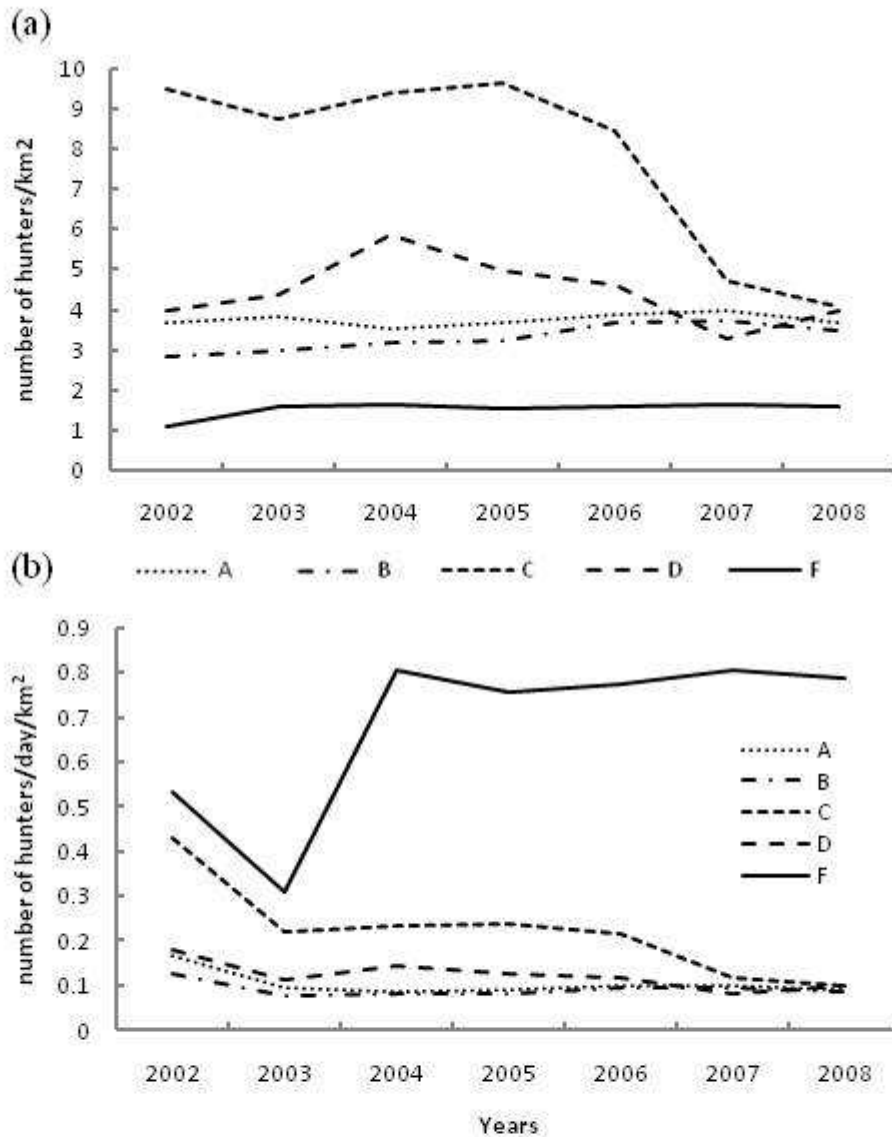


Figure 2. Hunting effort (number of hunters per km²) exerted on the bobwhite population in each zone of the BW area, South Florida, USA, presented as (a) total annual hunting effort and as (b) mean daily hunting effort. Note that hunting season in management zones A, B, C and D lasted approximately 40 days (late November-late December) whereas zone F was under hunting pressure for two days only in late January.

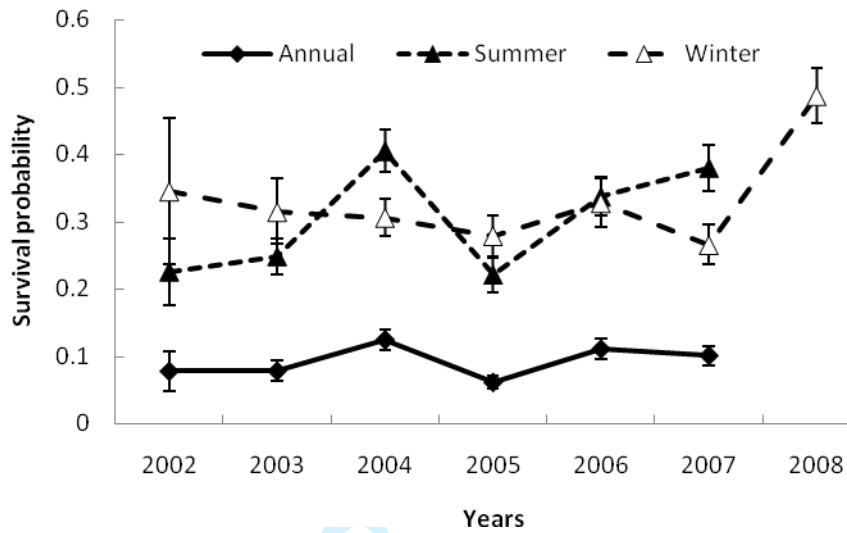


Figure 3. Year-to-year variations in annual (Oct-Sept), winter (Oct-March) and summer (April-Sept) survival (estimated from Cox's models with year as a covariate) of bobwhites in BW area, South Florida, USA.

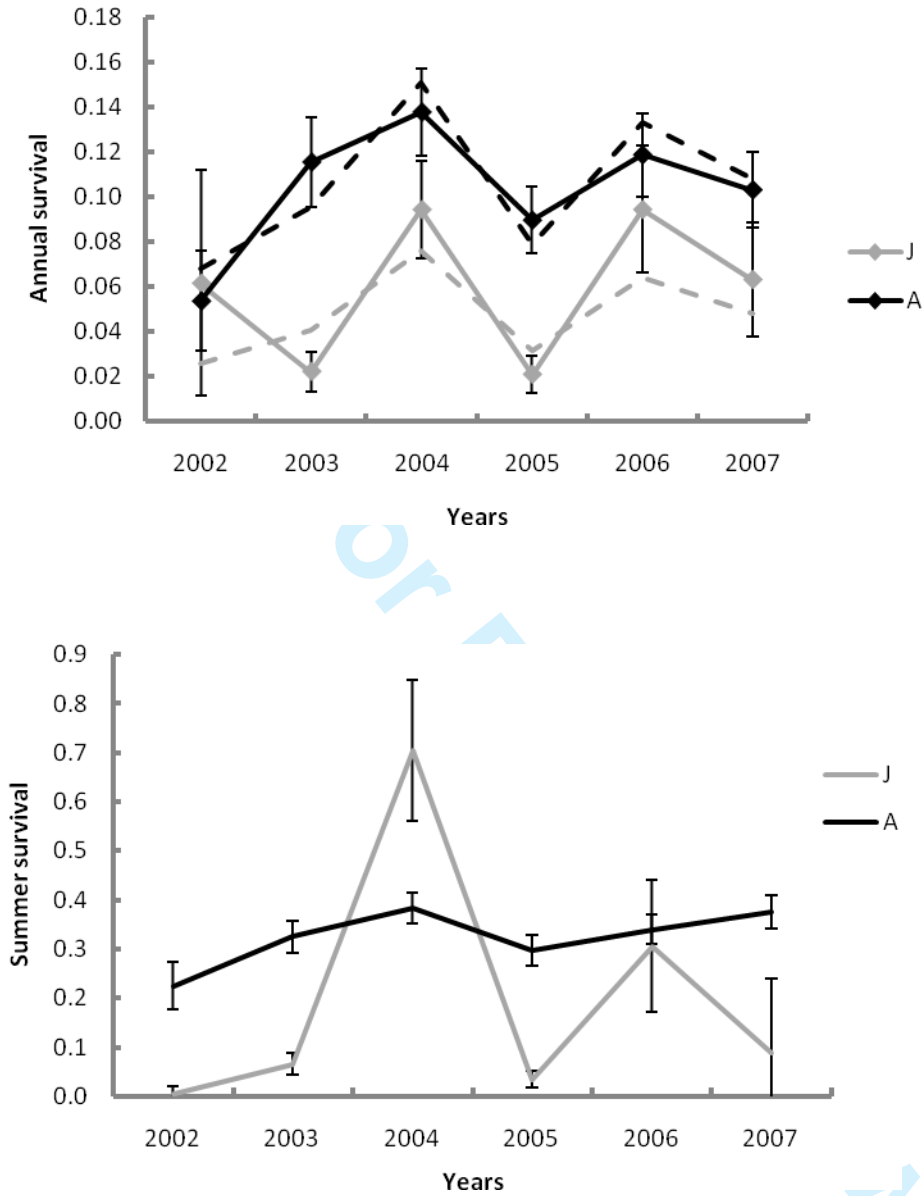


Figure 4. Annual and summer survival for juvenile (J) and adult (A) bobwhites in BW area, South Florida, USA, estimated from the model with additive effect of age and years (dashed line) or interaction effect (solid line).

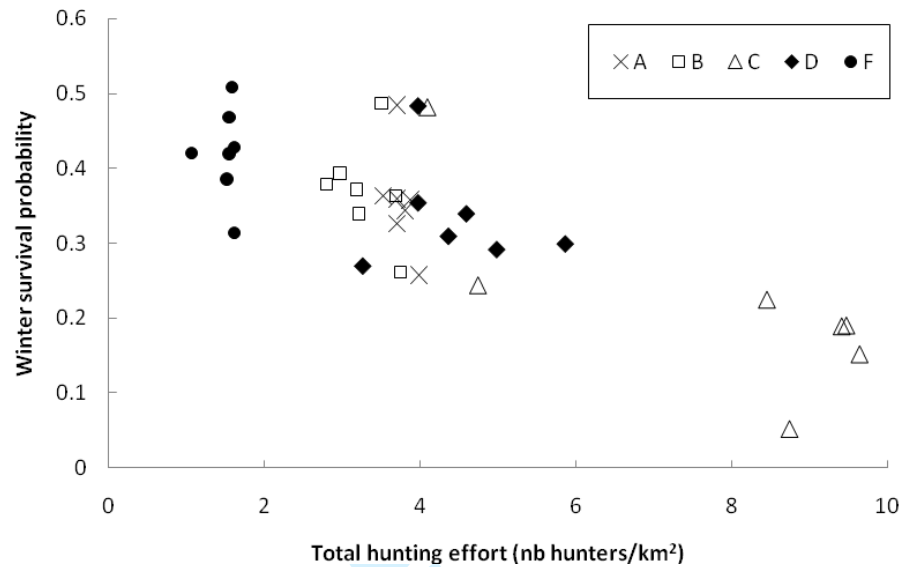


Figure 5. Winter survival of bobwhites on BW area, South Florida, USA in relation to total hunting effort (number of hunters per km²), based on the best model with an interactive effect of years and hunting effort. Hunting on the BW area occurred only during the winter season. For each zone (represented by a different symbol), seven points are given corresponding to each of the seven winters of the study period. Highest winter survival was recorded in 2008 for every zone.

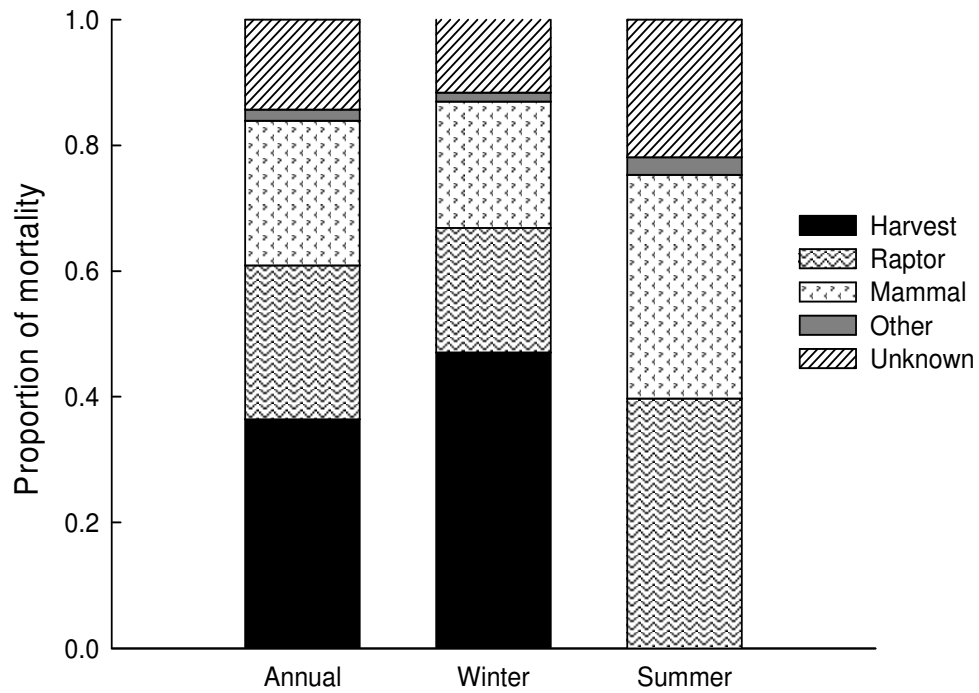


Figure 6. Proportion of annual, winter and summer mortality of bobwhites caused by harvesting, raptor and mammal predation, other (e.g., gout, predation by snakes) and unknown causes, on BW area, South Florida, USA. Proportion of mortality was calculated as: cause-specific mortality rate / (1-survival).

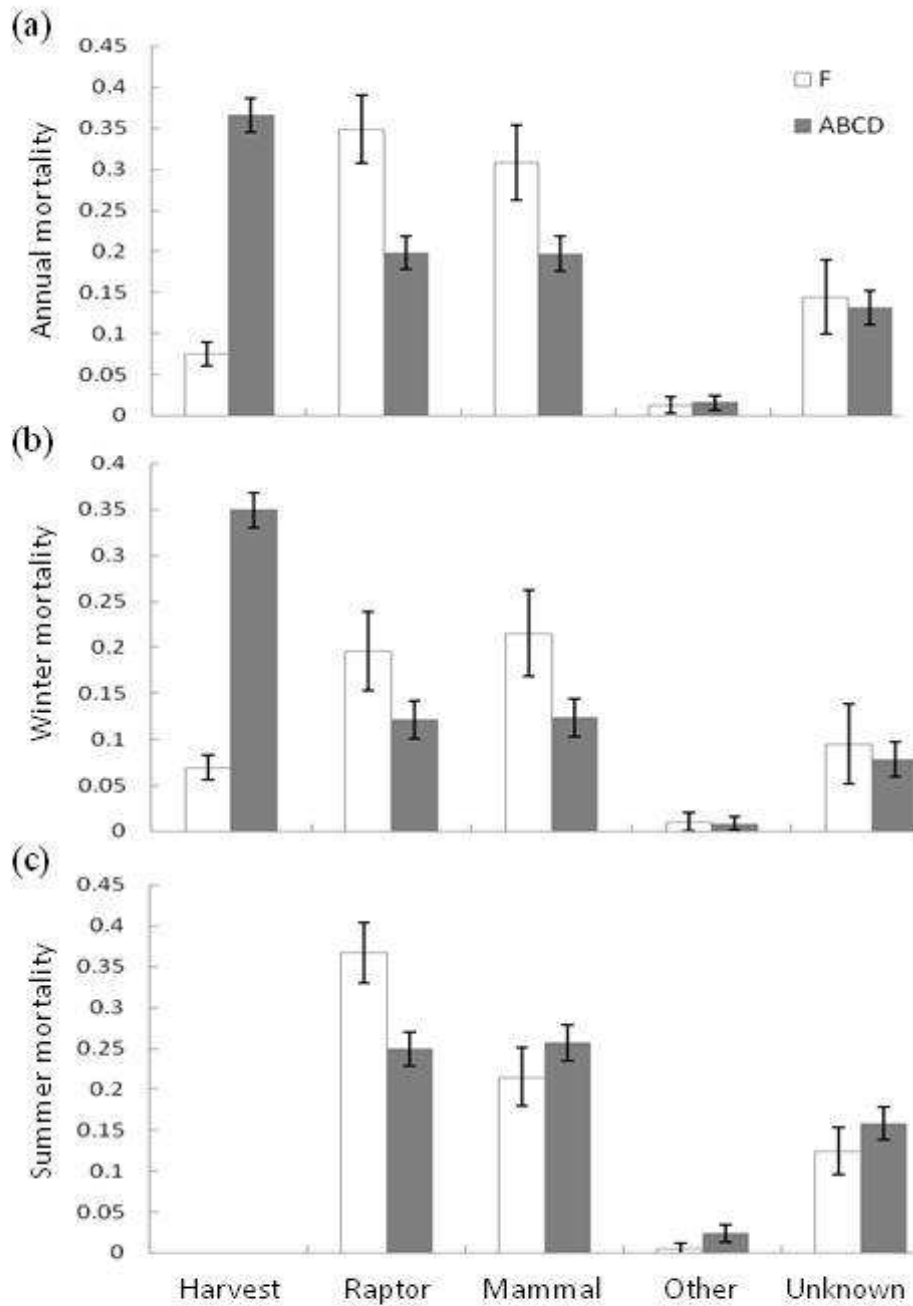


Figure 7. Cause-specific mortality rates of bobwhites in BW area, South Florida, USA. These are given for field trial (zone F) vs. other management zones combined (ABCD) on the annual (a), winter (b) and time summer (c) scale. Causes of mortality were harvesting, raptor or mammal predation, “other” (including snake predation) and unknown.