Original Article

Raptor Abundance and Northern Bobwhite Survival and Habitat Use

JOSHUA W. TURNER, *Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, MSC 218, Kingsville, TX 78363-8202, USA*

FIDEL HERNÁNDEZ,[1] *Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, MSC 218, Kingsville, TX 78363-8202, USA*

CLINT W. BOAL, *United States Geological Survey, Texas Cooperative Fish and Wildlife Research Unit, Texas Tech University, Lubbock, TX 79409, USA*

BART M. BALLARD, *Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, MSC 218, Kingsville, TX 78363-8202, USA*

FRED C. BRYANT, *Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, MSC 218, Kingsville, TX 78363-8202, USA*

DAVID B. WESTER, *Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, MSC 218, Kingsville, TX 78363-8202, USA*

ABSTRACT Predation risk has a profound influence on prey behavior and habitat use. The Rio Grande Plains ecoregion of Texas, USA, provides a unique opportunity to investigate changes in prey behavior because the ecoregion experiences a high influx of raptors every year during autumn migration. We used an 8-year data set (2000–2008) of radiocollared northern bobwhites (*Colinus virginianus*) and raptor abundance to test the hypothesis that bobwhites responded to increased raptor abundance via changes in woody-cover use at the home-range scale. Bobwhite survival was negatively correlated with raptor abundance, with red-tailed hawks (*Buteo jamaicensis*), and northern harriers (*Circus cyaneus*) accounting for 51% of the variability in bobwhite survival ($P < 0.010$). However, we documented no change in the amount of woody cover used by bobwhites in their home range between the raptor migration ($6.6\% \pm 0.5\%$; $n = 73$ bobwhites) and non-migration periods ($7.1\% \pm 0.4\%$; $n = 105$ bobwhites; $P = 0.490$). In addition, bobwhites that survived the raptor migration period used similar amounts of woody cover within their home range ($6.3\% \pm 0.6\%$, $n = 58$ bobwhites) compared with those dying during the migration period ($6.8\% \pm 0.4\%$, $n = 100$ bobwhites; $P = 0.530$). Our data suggest that bobwhites do not alter their use of woody cover at the home-range scale in response to increasing raptor abundance, but this does not preclude increased use of woody cover at the point-of-use scale. © 2014 The Wildlife Society.

KEY WORDS bobwhite, *Colinus virginianus*, habitat use, migration, northern bobwhite, predation, raptors, survival, Texas.

The risk of predation exerts a profound influence on prey behavior and space use (Lima and Dill 1990; Lima 1998*a*, *b*). Research suggests that prey will avoid areas of high predator density or high vulnerability in order to minimize predation risk (Lima 1998*a*, *b*), even if these behavioral changes result in reduced foraging opportunities (Bland and Temple 1990, Lima 1998*a*). A large body of theoretical and empirical evidence now exists on the trade-off between the benefit of minimizing predation risk and the energetic cost of doing so (Lima 1998*b*). Understanding prey habitat use from a predation-risk framework therefore provides important insight into the adaptive value of habitat for wildlife (Lima 1998*a*, *b*, Thirgood et al. 2002).

Raptors pose a notable predation threat to northern bobwhite (*Colinus virginianus*; Rollins and Carroll 2001).

Raptors may account for 25–63% of annual mortality of bobwhites (Burger et al. 1995, Carter et al. 2002, Cox et al. 2004) and have been implicated in catastrophic declines of local populations (Jackson 1947). Bobwhites can minimize their risk of predation through their use of woody cover (Kopp et al. 1998, Hiller and Guthery 2005, Ransom et al. 2008).

Woody plants represent an important escape cover for northern bobwhite (Davis 1964, Exum et al. 1982, Roseberry and Klimstra 1984), and cover management therefore has been suggested as a means to reduce predation risk (Leopold 1933:240, Brennan 1991). Because habitat heterogeneity can affect predator efficiency (Bowman and Harris 1980), the spatial and temporal distribution of woody cover within a landscape may influence the population dynamics of northern bobwhite (Williams et al. 2000).

The Rio Grande Plains of Texas, USA (Gould 1975) is an ecological region that provides a unique opportunity to investigate northern bobwhite habitat-use decisions from a predation-risk framework. The ecoregion is a mixed-brush savannah characterized by a large expanse of native, contiguous rangeland. Woody cover is abundant in the Rio

Grande Plains and has increased considerably during the past 150–200 years (Scifres 1980, Archer 1994). Bobwhite populations in this ecoregion have remained relatively non-trending through time (Church et al. 1993, Hernández et al. 2002, Brennan 2007), although populations experience drastic fluctuations due to variable rainfall (Hernández et al. 2005). The ecoregion also lies within a major migration route of raptors. Thousands of North American raptors migrate through the Rio Grande Plains each year on their way to wintering territories in Central and South America (Reed et al. 2004). The ecoregion therefore experiences a dramatic influx of raptors every autumn that exposes bobwhite populations to a high diversity and abundance of a primary predator. This natural system provided the context for an interesting ecological inquiry, *how have bobwhites managed to cope, and sometimes thrive, in an environment where they are subject to periodic, dramatic influxes of their primary predator?* The objectives of our study were to 1) quantify the correlation between raptor abundance and bobwhite survival, 2) document changes in bobwhite use of woody cover in response to autumn migration of raptors, and 3) evaluate the influence of woody cover on bobwhite survival.

STUDY AREA

Our study was conducted on the Rio Grande Plains ecoregion of Texas (Gould 1975). This ecoregion was characterized by level to rolling land that was dissected by streams flowing into the Rio Grande or the Gulf of México (Scifres 1980). Mean annual rainfall in this area was 40–76 cm, with the greatest amount occurring in May and June (Correll and Johnston 1979). The ecoregion has experienced an increase in woody-plant coverage over the past 150–200 years (Scifres 1980, Archer 1994) and is characterized by large ranches with cattle production as a primary land use (Hernández et al. 2002). It is renowned for northern bobwhite hunting and historically has supported relatively stable northern bobwhite populations (Hernández et al. 2002, Brennan 2007).

Our study area was a private ranch (42,448 ha) located in the western portion of the Rio Grande Plains. We selected 3 study sites (405 ha each) that were contained within a commercial hunting lease (approx. 13,000 ha) on the ranch. Study sites were located in a north–south layout with approximately 5-km spacing between sites. The commercial hunting lease was managed specifically for northern bobwhite. Management practices included grazing manage-ment, brush management, prescribed fire, discing, and harvest management (Howard 2007).

Woody vegetation on the study sites consisted predomi-nantly of honey mesquite (*Prosopis glandulosa*), huisache (*Vachellia farnesiana farnesiana*), granjeno (*Celtis pallida*), lime prickyash (*Zanthoxylum fagara*), prickly pear cactus (*Opuntia engelmannii lindheimeri*), tasajillo (*Cylindropuntia leptocaulis*), and live oak (*Quercus virginiana*). Common grasses included little bluestem (*Schizachyrium scoparium*), paspalum (*Paspalum* spp.), Kleberg bluestem (*Dichanthium annulatum*), King Ranch bluestem (*Bothriochloa ischaemum*), buffelgrass (*Cenchrus ciliaris*), red lovegrass (*Eragrostis secundiflora*), gulf cordgrass (*Spartina spartinae*), and sandbur

(*Cenchrus incertus*). Predominant forbs were croton (*Croton* spp.), dayflower (*Commelina erecta*), partridge pea (*Chamae-crista fasciculata*), and sunflower (*Helianthus annuus*).

METHODS

Northern Bobwhite Survival and Habitat Use

We captured northern bobwhite using baited funnel-traps (Stoddard 1931) during January–December, 2000–2008. We weighed bobwhites and classified them by age and gender. We banded all bobwhites and attached a 6–7-g pendant-style transmitter (American Wildlife Enterprises, Monticello, FL) to birds weighing >150 g (Hernández et al. 2005). We continuously trapped to maintain ≥20 radiocollared northern bobwhites/study site ($n = 60$ total) throughout the year. Radiocollared birds were located by homing (White and Garrott 1990) 3 times/week. We obtained Universal Transverse Mercator coordinates of radiocollared bobwhites during tracking sessions using a hand-held Global Position-ing System (Etrex model; Garmin Global Positioning Systems, Olathe, KS). We conducted this research under a Texas A&M University-Kingsville Institutional Animal Care and Use Committee protocol and permit (no. 2003-3-3).

Turner (2008) determined that peak winter occupancy of raptors (i.e., autumn migration period) occurred on our study area during September–February. Thus, we calculated monthly bobwhite survival (pooled across study areas) during this period to examine relationships with raptor abundance. We calculated monthly bobwhite survival using the Kaplan–Meier survival estimator (Kaplan and Meier 1958) with a staggered-entry approach (Pollock et al. 1989) in Program STAGKAM (Kulowiec 1989). We excluded from survival calculation individuals dying within 7 days of capture, to account for mortalities possibly related to stress from trapping and radiocollaring (Pollock et al. 1989, Burger et al. 1995). We also excluded any individuals succumbing to harvest because our interest was in natural predation.

We also calculated home ranges of northern bobwhite during raptor migration (Sep–Feb) and non-migration (Mar–Aug) periods. We calculated home ranges using 95% fixed-kernel estimator and the Animal Movements extension (Hooge and Eichenlaub 2000) in Arc View 3.2. We calculated home ranges only for bobwhites having ≥15 locations during a particular time period (i.e., migration or non-migration period) to minimize potential sample size bias on home range size (Haines et al. 2009). We then estimated percent woody canopy cover within each home range using 1-m resolution, color-infrared imagery obtained from National Agriculture Imagery Program. We used supervised classifi-cation of color-infrared imagery in ERDAS Imagine 8.7 (Leica, Norcross, GA) to obtain estimates of percent woody canopy cover within home ranges. We conducted ground testing of the vegetation map and determined that supervised classification was 86% accurate (Lawson 2009).

Raptor Abundance

We estimated relative abundance of raptors using roadside surveys during January–December, 2000–2008. Raptor surveys involved 3 observers who searched for raptors

from a slow-moving vehicle (24 km/hr) along a 23.3-km route that spanned the 13,000-ha study area. Raptor surveys were conducted between 0800 and 1100 hrs every 15 days throughout the 8-year study period. Observers used hand-held binoculars (Bausch & Lomb 10×50 mm, Prospect Heights, IL) to aid in identification of all raptors. We recorded the species and number observed; unidentifiable species were categorized as unknown. Our measure of raptor abundance was an index and therefore subject to the limitations of indices; this measure was sufficient to detect changes in relative abundance of raptors and therefore met the needs of our study (Turner 2008).

Because not all raptors posed a threat to bobwhites, we identified a subset of raptors that were capable of preying on bobwhites based on their body size, diet, hunting tactics, and agility. We termed this group "threat-specific raptors" and they consisted of Cooper's hawk (*Accipiter cooperii*), sharp-shinned hawk (*A. striatus*), northern harrier (*Circus cyaneus*), merlin (*Falco columbarius*), peregrine falcon (*F. peregrinus*), Harris' hawk (*Parabuteo unicinctus*), red-tailed hawk (*Buteo jamaicensis*), white-tailed hawk (*B. albicaudatus*), Swainson's hawk (*B. swainsoni*), and great-horned owl (*Bubo virginianus*). Species occurring on our study area but not considered a threat to bobwhites and therefore not included in the analysis were red-shouldered hawk (*Buteo lineatus*), broad-winged hawk (*B. platypterus*), Mississippi kite (*Ictinia mississippiensis*), white-tailed kite (*Elanus leucurus*), crested caracara (*Caracara plancus*), and American kestrel (*Falco sparverius*). Red-shouldered and broad-winged hawks were not considered to pose a threat to bobwhites because their diet consists mostly of non-avian prey items (amphibians, reptiles, and small mammals), and they have not been documented preying on quail (Stoddard 1931). Mississippi kites and white-tailed kites also posed minimal threat to bobwhites because of their mostly non-avian diet (insects and small mammals; Dunk 1995, Parker 1999). American kestrels are too small, relative to the body mass of a bobwhite, to pose a meaningful threat (Smallwood and Bird 2002). We calculated mean relative abundance (no. of raptors/km) by month for each species in the threat-specific group.

Statistical Analysis

We chose candidate models to identify raptor species whose abundance was related to northern bobwhite mortality on the basis of an *a priori* decision to examine 1) all possible single-predator species models, 2) all possible 2-predator species models that included the best single species, and 3) all possible 3-predator species models that included the 2 best species; 30 models were evaluated. We used 2 approaches for model selection. One approach used stepwise multiple regression (Kutner et al. 2004) to select raptor species that were most highly related to monthly survival of northern bobwhite; we used forward selection and entered and retained variables at a 5% significance level. A second approach was based on information theory (Burnham and Anderson 2002). Both approaches yielded similar results by identifying the same "best model."

We used the Durbin–Watson test (1951) to assess autocorrelation of errors associated with successive survival estimates, and the Yule–Walker method (Gallant and Goebel 1976) to estimate the autocorrelation coefficient. When the Durbin–Watson test was significant, we used the method of Cochrane and Orcutt (1949) to transform both dependent and independent variables, and we repeated the Durbin–Watson test on the transformed variables. In all cases, autocorrelation was eliminated after one iteration (Montgomery and Peck 1982). For the species identified as important by multiple regression analysis, we used Pearson's correlation to calculate a correlation coefficient by year between bobwhite survival and raptor relative abundance.

We used a 2-independent-sample Student's *t*-test by year to compare percent woody cover of home ranges between bobwhites surviving the migration period and those dying during the migration. For bobwhites that survived between periods, we used a paired *t*-test to compare the change in percent woody cover of home ranges from the non-migration to migration period. We conducted all analyzes using SAS (version 9.2; SAS Institute, Inc., Cary, NC).

RESULTS

Mean monthly relative abundance of threat-specific raptors approximately doubled (93% increase) from the non-migration period (41.3 ± 5.4 raptors/100 km) to the migration period (79.9 ± 8.4 raptors/100 km; Table 1). Merlins exhibited the greatest increase (972%) between these periods, followed by northern harriers (462%) and red-tailed hawks (234%). The most abundant raptor species during the migration period were red-tailed hawk (28.7 ± 3.6 raptors/100 km), white-tailed hawk (14.6 ± 1.9 raptors/100 km), northern harrier (14.6 ± 2.9 raptors/100 km), and Harris' hawk (6.9 ± 1.4 raptors/100 km; Table 1).

We calculated monthly survival estimates based on 1,430 radiocollared bobwhites during the 8-year study. Monthly survival ranged from 0.57 to 0.99 (mean $\pm$ SE: 0.84 ± 0.02). Bobwhite survival was related negatively to mean monthly relative abundance of red-tailed hawks ($r^2 = 0.40$, $P < 0.001$; Fig. 1A) and northern harriers ($r^2 = 0.38$, $P < 0.001$; Fig. 1B; Table 2). Together these 2 species explained 51% of the variation in monthly bobwhite survival (Table 2) and adding additional raptor species did not significantly ($P = 0.050$) improve model fit. This 2-species model was also the "best" model identified via AIC$_c$ comparisons; other models with support included a single-species model with red-tailed hawks (which was also the best single-species model based on r^2 value) and a 3-species model with red-tailed hawks, northern harriers, and sharp-shinned hawks (which was also the 3-variable for which, collectively, all 3 explanatory variables achieved the highest significance; Table 2). A significant correlation between bobwhite survival and relative abundance of red-tailed hawks and northern harriers coincided only in 1 of 8 years (autumn–winter of 2006–2007; Table 3).

We calculated home ranges for 227 bobwhites during raptor migration period (14.4 ± 0.6 ha) and 265 bobwhites during the non-migration period (mean $\pm$ SE: 22.0 ± 1.3 ha). Sample size of bobwhites for the home-range analysis was smaller than the sample size for the survival analysis because

Table 1. Relative abundance (no./100 km) of threat-specific raptor species during spring–summer (Mar–Aug) and autumn–winter (Sep–Feb), Brooks County, Texas, USA, 2000–2008. Threat-specific raptors were defined as raptors capable of preying on northern bobwhite (*Colinus virginianus*).

Season		SSHA[a]		COHA[a]		RTHA[a]		WTHA[a]		SWHA[a]		HAHA[a]		NOHA[a]		PEFA[a]		MERL[a]		GHOW[a]		UKWN[a]		All species	
Year	n	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Spring–summer																								
2001	6	0.0	0.0	1.0	0.4	6.3	2.4	13.0	2.8	0.0	0.0	1.0	1.0	4.3	3.9	1.0	0.7	0.3	0.3	0.7	0.4	6.8	3.5	34.5	10.5
2002	6	0.0	0.0	0.7	0.4	7.5	4.3	7.7	1.8	7.2	7.2	0.0	0.0	1.7	1.1	1.0	1.0	0.0	0.0	2.8	1.4	3.7	2.4	32.2	12.2
2003	6	0.0	0.0	1.7	0.8	3.7	2.1	9.0	1.8	0.0	0.0	1.5	1.5	0.0	0.0	0.0	0.0	0.0	0.0	3.0	2.0	0.7	0.4	19.5	6.2
2004	6	0.0	0.0	4.2	2.6	8.0	2.1	23.0	3.5	0.0	0.0	8.7	2.9	0.7	0.7	0.0	0.0	0.0	0.0	0.3	0.3	11.2	3.0	56.0	5.7
2005	6	0.0	0.0	5.2	1.7	13.5	7.2	29.8	12.5	0.0	0.0	7.5	3.2	1.8	1.5	0.0	0.0	0.0	0.0	2.0	0.9	7.7	3.7	67.5	28.1
2006	6	1.0	0.7	0.8	0.5	13.0	4.7	8.8	1.7	5.7	5.7	2.7	1.3	3.3	0.8	0.0	0.0	0.0	0.0	1.0	0.4	8.0	2.7	44.3	7.5
2007	6	0.0	0.0	0.0	0.0	8.2	3.8	9.0	2.9	0.0	0.0	6.8	5.2	6.3	5.2	0.0	0.0	0.0	0.0	0.0	0.0	4.5	1.6	34.8	13.7
Pooled	42	0.1	0.1	1.9	0.5	8.6	1.5	14.3	2.2	1.8	1.3	4.0	1.1	2.6	1.0	0.3	0.2	0.0	0.0	1.4	0.4	6.1	1.1	41.3	5.4
Autumn–winter																								
2000	5	1.4	0.6	3.6	1.5	30.6	1.9	16.8	6.1	0.4	0.4	4.4	2.5	14.0	4.2	0.2	0.2	0.4	0.4	0.8	0.5	7.8	2.5	80.4	5.6
2001	6	0.0	0.0	0.7	0.4	19.7	6.8	7.2	2.7	0.0	0.0	0.0	0.0	4.2	1.9	0.0	0.0	1.0	0.7	0.7	0.4	10.5	2.9	43.8	9.7
2002	6	0.0	0.0	0.0	0.0	12.8	5.2	11.2	3.7	0.0	0.0	1.3	0.8	2.5	1.5	0.0	0.0	0.7	0.4	1.5	1.5	1.5	1.5	38.0	14.7
2003	6	0.0	0.0	3.0	1.4	15.7	3.9	21.2	4.7	0.0	0.0	0.5	0.5	6.7	3.6	0.0	0.0	0.5	0.5	0.8	0.8	8.3	2.7	56.7	11.7
2004	6	0.0	0.0	8.5	1.8	41.8	12.6	26.2	10.5	0.0	0.0	21.2	5.7	10.0	2.3	0.0	0.0	0.0	0.0	1.3	1.0	14.2	2.8	123.2	30.6
2005	6	0.0	0.0	3.8	1.4	24.5	6.6	14.3	1.5	0.0	0.0	2.3	0.9	4.3	2.9	0.0	0.0	0.0	0.0	1.5	0.6	4.5	1.9	55.3	10.2
2006	6	1.8	1.5	5.8	2.8	56.8	17.3	11.3	4.3	0.0	0.0	15.0	3.6	45.3	11.3	0.0	0.0	0.8	0.5	3.2	1.1	6.5	3.3	146.7	30.6
2007	6	0.0	0.0	0.8	0.8	27.8	6.3	9.3	2.6	0.0	0.0	10.3	3.4	29.7	9.8	0.0	0.0	0.7	0.4	0.3	0.3	16.0	4.1	95.0	22.2
Pooled	47	0.4	0.2	3.3	0.6	28.7	3.6	14.6	1.9	0.0	0.0	6.9	1.4	14.6	2.9	0.0	0.0	0.5	0.2	1.3	0.3	9.5	1.2	79.9	8.4

[a] SSHA, sharp-shinned hawk; COHA, Cooper's hawk; RTHA, red-tailed hawk; WTHA, white-tailed hawk; SWHA, Swainson's hawk; HAHA, Harris' hawk; NOHA, northern harrier; PEFA, peregrine falcon; MERL, merlin; GHOW, great-horned owl; UKWN, unknown.

fewer bobwhites survived sufficient time to accumulate our criteria for the minimum number of locations required for home range calculation. The percentage of woody cover within the home range of bobwhites was similar between the

raptor migration (6.6% ± 0.5%, $n = 73$) and non-migration periods (7.1% ± 0.4%, $n = 105$; $P = 0.490$). Bobwhites that survived the raptor migration period used similar amounts of woody cover (6.3% ± 0.6%, $n = 58$) compared with those dying during the migration period (6.8% ± 0.4%, $n = 100$; $P = 0.530$). In addition, we documented no change in use of percent woody cover from the non-migration to migration period (mean difference: 0.30% ± 0.27%; $t = 1.11$, df = 144, $P = 0.270$).

DISCUSSION

Relative abundance of red-tailed hawk and northern harrier accounted for a moderate amount of the variability in bobwhite survival. This general relationship is consistent with past game-bird research; some raptor species can be a significant source of mortality for many galliform species (Snyder 1985, Riley et al. 1994, Martin et al. 2001). However, although it is likely that raptor abundance influenced bobwhite survival, we acknowledge that other factors correlated with season, such as changes in herbaceous vegetation structure or food availability also may have influenced survival. For example, herbaceous vegetation structure can decrease with season because of freezes or drought (Lehmann 1984), which could increase bobwhite vulnerability to predation. The extent to which these other factors influenced bobwhite survival is unknown but plausible.

The negative relationship between abundance of northern harriers and bobwhite survival is not surprising. Northern harriers are capable and common predators of bobwhites (Rollins and Carroll 2001) and other game birds (Haukos and Broda 1989, Thirgood et al. 2000). Jackson (1947) reported that northern harriers were the proximate cause of mortality and reduction of a bobwhite population irruption in northwest Texas. The relationship between red-tailed
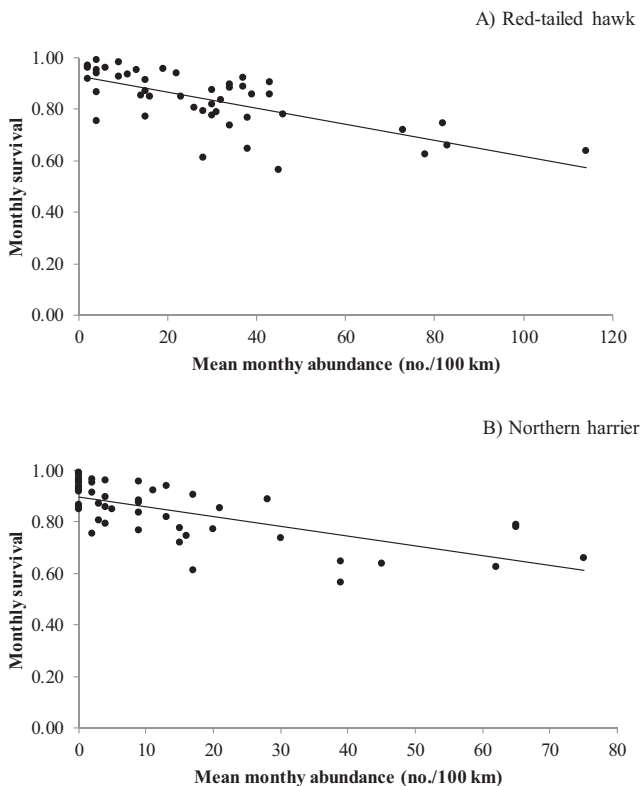

Figure 1. Relationship between monthly survival of northern bobwhite (*Colinus virginianus*; y-axis) and mean monthly abundance of (A) red-tailed hawk (*Buteo jamaicensis*; x-axis) and (B) northern harrier (*Circus cyaneus*; x-axis), Brooks County, Texas, USA, September–February, 2000–2008.

Table 2. Results of 1-, 2-, and 3-species models used to identify raptor species most highly related to monthly survival of northern bobwhite (*Colinus virginianus*), Brooks County, Texas, USA, September–February, 2000–2008. Coefficients of determination are adjusted (coeff. followed by an asterisk are unadjusted because adjustment resulted in a negative estimate); $n = 47$ for initial analysis and $n = 46$ in analysis that accounted for autocorrelation; w_i = Akaike weight; Δ_i = change in AIC_c.

Species	R^2	β	SE	$P > t$	w_i	Δ_i
Red-tailed hawk	0.40	−0.284	0.051	<0.0001	0.102	1.097
Northern harrier	0.38	−0.367	0.069	<0.0001	0.004	7.585
Harris' hawk	0.07	−0.317	0.152	0.042	0.000	19.040
White-tailed hawk	0.05	−0.179	0.101	0.084	0.000	18.440
Cooper's hawk	0.02	−0.475	0.331	0.158	0.000	19.692
Sharp-shinned hawk	0.01*	−0.674	0.983	0.496	0.000	21.748
Unknown	0.02	−0.237	0.174	0.179	0.000	20.350
Merlin	0.001*	−0.272	1.101	0.806	0.000	21.682
Great-horned owl	0.01	−0.139	0.561	0.806	0.000	21.757
Peregrine falcon	0.00*	0.293	9.759	0.976	0.000	21.748
Swainson's hawk	0.00*	0.293	9.759	0.976	0.000	21.748
Red-tailed hawk	0.51	−0.201	0.062	0.002	0.177	0
Northern harrier		−0.201	0.080	0.016		
Red-tailed hawk	0.40	−0.288	0.051	<0.0001	0.045	2.737
Sharp-shinned hawk		−1.008	0.835	0.234		
Red-tailed hawk	0.40	−0.284	0.052	<0.0001	0.019	4.502
Great-horned owl		−0.025	0.499	0.960		
Red-tailed hawk	0.40	−0.297	0.057	<0.0001	0.023	4.100
Unknown		0.070	0.165	0.672		
Red-tailed hawk	0.39	−0.286	0.051	<0.0001	0.025	3.902
Merlin		−0.670	0.962	0.490		
Red-tailed hawk	0.39	−0.297	0.057	<0.0001	0.020	4.318
White-tailed hawk		0.047	0.099	0.634		
Red-tailed hawk	0.39	−0.299	0.063	<0.0001	0.021	4.242
Harris' hawk		0.057	0.154	0.711		
Red-tailed hawk	0.39	−0.279	0.053	<0.0001	0.022	4.215
Cooper's hawk		−0.112	0.290	0.701		
Red-tailed hawk	0.39	−0.285	0.051	<0.0001	0.019	4.493
Peregrine falcon		1.529	15.41	0.921		
Red-tailed hawk	0.39	−0.285	0.051	<0.0001	0.019	4.493
Swainson's hawk		1.529	15.41	0.921		
Red-tailed hawk	0.53	−0.215	0.069	0.003	0.058	2.224
Northern harrier		−0.207	0.082	0.015		
Harris' hawk		0.071	0.146	0.629		
Red-tailed hawk	0.53	−0.197	0.065	0.004	0.052	2.449
Northern harrier		0.201	0.081	0.017		
Cooper's hawk		−0.061	0.280	0.828		
Red-tailed hawk	0.51	−0.195	0.067	0.006	0.050	2.530
Northern harrier		−0.207	0.080	0.013		
Unknown		−0.036	0.156	0.818		
Red-tailed hawk	0.50	−0.185	0.074	0.016	0.054	2.386
Northern harrier		−0.217	0.087	0.016		
White-tailed hawk		−0.041	0.101	0.686		
Red-tailed hawk	0.50	−0.200	0.062	0.002	0.052	2.466
Northern harrier		−0.203	0.080	0.016		
Peregrine falcon		8.160	34.34	0.813		
Red-tailed hawk	0.50	−0.200	0.062	0.002	0.052	2.466
Northern harrier		−0.203	0.080	0.016		
Swainson's hawk		8.160	34.34	0.813		
Red-tailed hawk	0.50	−0.202	0.064	0.003	0.050	2.510
Northern harrier		−0.201	0.083	0.020		
Merlin		−0.060	0.986	0.952		
Red-tailed hawk	0.50	−0.201	0.062	0.002	0.051	2.503
Northern harrier		−0.206	0.081	0.016		
Great-horned owl		0.072	0.501	0.887		
Red-tailed hawk	0.49	−0.209	0.063	<0.0001	0.086	1.438
Northern harrier		−0.190	0.082	0.025		
Sharp-shinned hawk		−0.764	0.814	0.353		

hawks and bobwhite survival, however, is surprising. Red-tailed hawks generally are not considered a primary predator of bobwhites, although they may occasionally prey on quail (Stoddard 1931). Red-tailed hawks are presumed to lack the agility and speed of the principal avian predators of quail (e.g., accipiters, northern harriers) which would be required to pose a notable threat to bobwhites. One explanation for this finding is that the relationship is spurious. The timing of peak winter occupancy of raptors in our study area generally coincided among species and therefore relative abundance

Table 3. Correlation analysis between monthly survival of northern bobwhite (*Colinus virginianus*) and relative abundance (no./km) of 2 raptor species, Brooks County, Texas, USA, September–February, 2000–2008.

		Red-tailed hawk		Northern harrier	
Year	*n*	*r*	*P*-value	*r*	*P*-value
Oct 2000–Feb 2001	5	0.63	0.26	0.08	0.90
Sep 2001–Feb 2002	6	−0.93	0.01	−0.11	0.84
Sep 2002–Feb 2003	6	−0.88	0.02	−0.69	0.13
Sep 2003–Feb 2004	6	−0.75	0.09	−0.96	0.002
Sep 2004–Feb 2005	6	−0.83	0.04	−0.66	0.16
Sep 2005–Feb 2006	6	0.02	0.97	0.39	0.45
Sep 2006–Feb 2007	6	−0.94	0.01	−0.82	0.05
Sep 2007–Feb 2008	6	−0.73	0.10	−0.37	0.47

among raptors inherently was correlated (Turner 2008). Relative abundance of red-tailed hawks and northern harriers pooled across years was highly correlated ($r = 0.70$) in our study. Thus, it is possible that the negative relationship between red-tailed hawk abundance and bobwhite survival was an artifact of such high association with northern harriers. Although this is a possibility and may account partially for our findings, we believe that red-tailed hawks did influence bobwhite survival in our study for several reasons.

We documented a significant relationship between bobwhite survival and relative abundance of red-tailed hawks in 4 of 8 years and relative abundance of northern harriers in 2 of 8 years. These relationships coincided between the 2 species in only 1 year (autumn–winter of 2006–2007). Thus, red-tailed hawk abundance was negatively related with bobwhite survival during several years when there was no significant relationship detected between northern harrier abundance and bobwhite survival. In addition, Stoddard (1931) suggested that red-tailed hawks were not a concern for bobwhite populations unless they became numerous. Red-tailed hawks were the most abundant raptor in our study during autumn–winter, being 2–70 times more abundant than any other raptor species. Moreover, although the diet of red-tailed hawks consists primarily of small mammals and reptiles with some birds (Fitch et al. 1946), red-tailed hawks are generalists and are known to increase their intake of avian prey based on availability (Orians and Kuhlman 1956). Kane (2012) conducted a resource-partitioning study of 5 raptor species on our study area during our study. He documented that the percent of avian prey in the red-tailed diet (based on prey deliveries to nestlings) varied considerably, decreasing from 21% to 6% between 2 years. Coincidentally, bobwhite densities on the study area, a proxy of grassland bird abundance, also decreased from 2.94 bobwhites/ha to 1.83 bobwhites/ha during the same time period (Rusk et al. 2007). Red-tailed hawks therefore appeared to adjust their diet based on availability of avian prey (Kane 2012). Collectively, these observations provide evidence that the negative relationship between red-tailed hawk abundance and bobwhite survival may not be spurious but, rather, that red-tailed hawks may have contributed to bobwhite mortality during our study.

Regarding habitat use, bobwhites did not alter their use of woody cover at the home-range scale despite a near doubling of raptor relative abundance during autumn migration. In addition, bobwhites that survived the raptor migration period used similar amounts of woody cover within their home range as bobwhites dying during the migration period. These findings are consistent with those of Thirgood et al. (2002) who documented that neither vegetation height nor vegetation density explained any significant variation in red-grouse density or predation. Thirgood et al. (2002) also failed to detect habitat differences in the home ranges of red grouse that survived the winter compared those that were depredated. Thirgood et al. (2002) therefore concluded that little evidence existed at both the individual and population scales to indicate that habitat characteristics had any measurable effect on red grouse predation during winter. Williams et al. (2000), however, documented that increased selection of woody cover decreased natural predation (i.e., predation not due to hunting) on bobwhites and considered the selection of woody cover to be an important variable in bobwhite survival. The study areas of Williams et al. (2000) were a cropland site and a rangeland site with minimal amounts of woody cover (3% and 4%, respectively), and brush patches on the rangeland site consisted of few, large patches. Brush cover on our study sites was considerably greater (10–30%) and well-interspersed (DeMaso 2008). Thus, it is possible that woody cover on our study area occurred at a level and distribution sufficient to meet the escape-cover needs of bobwhites from a predation-risk standpoint.

Another possibility is that bobwhites did alter their use of woody cover in response to raptor abundance but the resolution of our woody-cover measurement was too coarse to detect a change. We monitored changes in woody-cover use at the home-range scale but not the point-of-use scale. It is possible that bobwhites increased their time spent in woody cover during the day without changing the overall location of their home range. If this was the case, then the percentage of woody cover at the home-range scale would not change. There is evidence that selection for amount of woody cover may vary between the point-of-use scale and home-range scale. Kopp et al. (1998) documented that bobwhites in southern Texas selected for >20–60% woody cover at flushing and landing points. Ransom et al. (2008) reported that locations of radiocollared bobwhites in northern Texas consisted of 30% woody cover. Perkins (2012) documented that percent woody cover at landing points varied depending on threat type (researcher, hunter,

mammalian, and raptor), with bobwhites using greater amounts of woody cover at landing points when pursued by a raptor (56%) than when responding to other threat types (<15%). Bobwhite home ranges in our study contained about 7% woody cover, which was considerably lower than the percentage of woody cover reported for individual points (Kopp et al. 1998, Ransom et al. 2008, Perkins 2012) but within the range (5–30%) recommended for bobwhites (Lehmann 1984, Fulbright and Guthery 1995, Hernández and Guthery 2012).

MANAGEMENT IMPLICATIONS

Our finding that red-tailed hawks explained the most variability in bobwhite survival is notable given that red-tailed hawks generally are not considered primary predators of quail. Our data suggested that bobwhites did not alter their use of woody cover at the home-range scale in response to increasing raptor abundance, but this does not preclude increased use of woody cover at the point-of-use scale. Woody cover provides important escape and thermal cover for bobwhites (Hiller and Guthery 2005) and preserving a sufficient quantity and distribution should enhance survival. Based on this and prior research, a landscape consisting of 5–30% woody cover occurring as well-distributed clusters of dense woody plants should meet the needs of bobwhites (Hernández and Guthery 2012).

ACKNOWLEDGMENTS

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