



Research Article

Northern Bobwhite Predator Avoidance Behavior in Response to Varying Types of Threat

REBECCA PERKINS,¹ Department of Natural Resources, Texas Tech University, Box 42125, Lubbock, TX 79409, USA

CLINT BOAL, U.S. Geological Survey, Texas Cooperative Fish and Wildlife Research Unit, Texas Tech University, Agricultural Sciences Room 218, Texas Tech University, Lubbock, TX 79409, USA

DALE ROLLINS, Rolling Plains Quail Research Ranch, Texas Agrilife Research and Extension Center, San Angelo, TX 76901, USA

ROBERT M. PEREZ, Texas Parks and Wildlife Department, La Vernia, TX 78121, USA

ABSTRACT The flight behavior and cover use of northern bobwhite (*Colinus virginianus*) have been examined in several studies, but the current data lack quantitative measures of how bobwhites respond to natural threats. We examined aspects of bobwhite behavior in response to 4 threat categories: researcher, hunter, raptor, and mammal. We found that bobwhite flight distance is best predicted by threat type and covey size, and bobwhite flight speed is best predicted by threat type. Bobwhites flushed by the hunter threat and the raptor threat selected for significantly taller obstruction at landing sites than was randomly available, with average heights of 6.2 cm taller ($P=0.034$), and 38.1 cm taller ($P<0.001$), respectively. Raptor-flushed bobwhites also selected for significantly denser shrub cover (42.2%, $P<0.001$) and a lower angle of obstruction (70.4° , $P<0.001$) at landing points than was randomly available. In the process of data collection, we also observed bobwhite roost locations have lower visual height obstruction (7.3 cm, $P=0.03$), lower shrub intercept (10.1%, $P=0.02$), and greater angles of obstruction (18.5° , $P=0.005$) than bobwhite diurnal locations; this may facilitate escape from nocturnal mammalian predators. Our results suggest that bobwhite escape strategies and cover use vary among threat types. These results support current management recommendations of creating a patchwork of vegetation covers for bobwhites but also suggest how a more complete understanding of bobwhite behavior would improve management and conservation efforts. © 2014 The Wildlife Society.

KEY WORDS *Colinus virginianus*, cover selection, habitat management, northern bobwhite, predation, predator avoidance behavior, Texas.

Northern bobwhites (*Colinus virginianus*; hereafter, bobwhite) are of considerable economic value to many communities (Burger et al. 1999, Conner 2007, Dodd 2009); however, steep population declines throughout their entire range have prompted conservation concern (Brennan 1991, Burger et al. 1999). Negative population trends have been attributed to habitat loss, habitat fragmentation, increased use of exotic grasses (e.g., bermudagrass [*Cynodon dactylon*]), and increased cattle grazing (Guthery 2000, Lusk et al. 2002). Increased predation from avian and mammalian predators related to habitat fragmentation and degradation also is thought to depress bobwhite populations (Mueller et al. 1999, Rollins and Carroll 2001, Staller et al. 2005). Though substantial attention has been given to depredation of nests and chicks, less information exists on predation of juvenile and adult birds (Hernandez and Peterson 2007). Burger et al. (1995) and Cox et al. (2004) investigated causes of mortality of

bobwhites in Missouri and western Oklahoma, respectively, and found avian predators to be the most significant source of winter mortality, followed by hunter harvest and mammalian predators. These studies examined predatory threats but did not address predator avoidance strategies used by bobwhites.

Kassinis and Guthery (1996) and Perez et al. (2002) studied distance and speed of bobwhite flights in southern Texas. These data served as the basis for Kassinis and Guthery's bobwhite-focused landscape management recommendations. Accordingly, they suggested that no point on the ground should be >100 m from escape cover. In contrast, Stoddard (1931:181) suggested no point should be >200 m from escape cover. This disparity relates to the differences in landscape. Guthery (1999) introduced the concept of slack, or the amount of variation within the range of vegetation communities suitable as habitat for bobwhites. Because Guthery (1999) determined bobwhites have a large amount of slack in their range-wide habitat, habitat-associated behaviors (e.g., average flight distance) likely vary along the same spatial scales.

The slack-related behavior gradient of bobwhites indicates that their behavior may also vary with other external stimuli. For example, redshanks (*Tringa totanus*), lesser prairie-

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¹E-mail: becki.perkins@ttu.edu

chickens (*Tympanuchus pallidicinctus*), and mallard ducklings (*Anas platyrhynchos*) are able to recognize different predation risks and adjust their threat avoidance behaviors accordingly (Cresswell 1996, Behney et al. 2011, Dessborn et al. 2012). We hypothesized that bobwhites too display threat-dependent responses. Although bobwhite escape behavior may initially appear to simply be a flush-and-fly tactic regardless of threat type, this may be an oversimplification of what could be a more complex behavior. If bobwhites do engage in threat-specific responses, lacking an understanding of these responses could inhibit management efforts. For example, Stoddard (1931), Kassinis and Guthery (1996), and Perez et al. (2002) observed escape behavior from only 1 type of threat, anthropogenic disruption. This possible bias may overlook any risk-specific escape behavior bobwhite may display and thus overlook possible management regimes that would complement such varying escape strategies. Thus, we quantitatively assessed bobwhite escape strategies in response to different threats, and characterized their selection of escape cover from the threats. Our goal was to study the escape behavior of bobwhites and to incorporate such knowledge to improve current habitat management strategies.

STUDY AREA

We worked on the entirety of the Rolling Plains Quail Research Ranch (hereafter, RPQRR) in Fisher County, Texas. The RPQRR is a not-for-profit 1,618-ha ranch used for wildlife research and education along with limited hunting. Average temperatures ranged from 3°C in January to 35°C in July, and the area had an average yearly rainfall of 61.1 cm (National Oceanic and Atmospheric Administration; <http://www.ncdc.noaa.gov/cdo-web/search>; accessed 3 Mar 2012). Elevation on the RPQRR was 587–925 m above sea level. Topography of the study area consisted of rocky ridges interspaced by grassy plains. Soils were primarily comprised of Paducah loam, Miles sandy loam, Latom-Vernon complex, Woodward clay loam, and Wichita clay loam types (Natural Resources Conservation Service 2010; <http://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx>; accessed 6 Mar 2010).

Vegetation at RPQRR contained a high diversity of grasses and forbs. Dominant warm-season grasses were silver bluestem (*Bothriochloa saccharoides*) and sideoats grama (*Bouteloua curtipendula*), whereas Texas wintergrass (*Nasella leucotricha*) was the primary cool-season species (United States Department of Agriculture, Natural Resources Conservation Service Plant Database as source for botanical names; <http://plants.usda.gov>, accessed 6 Mar 2010). Common forbs within the area were western ragweed (*Ambrosia psilostachya*), field ragweed (*A. confertiflora*), annual sunflower (*Helianthus annuus*), and 3 species of croton (*Croton* spp.). Previous brush-control practices have limited shrub density in places but not in diversity. Woody plants at RPQRR included agarita (*Mahonia trifoliata*), gum bumelia (*Sideroxylon lanuginosum*), catclaw acacia (*Acacia greggii*), catclaw mimosa (*Mimosa pellita*), elbow-bush (*Forestiera pubescens*), fragrant mimosa (*M. borealis*), littleleaf sumac

(*Rhus microphylla*), live oak (*Quercus virginiana*), lotebush (*Ziziphus obtusifolia*), mesquite (*Prosopis glandulosa*), netleaf hackberry (*Celtis laevigata* var. *reticulata*), skunkbush sumac (*R. trilobata*), and wolfberry (*Lycium barbarum*). Cacti were abundant on the landscape and included Engelmann's pricklypear (*Opuntia engelmannii*), plains pricklypear (*O. polyantha*), and tasajillo (*O. leptocaulis*).

METHODS

Capture and Flushing

We captured bobwhites September–November 2009 and 2010 in modified Stoddard quail traps (Schultz 1950). Traps sat along dirt roadways throughout the study site in locations that promoted the capture of individuals from each covey known from RPQRR-wide surveys (D. Rollins, Rolling Plains Quail Research Ranch, personal observation). We banded all birds with a uniquely numbered aluminum leg band. If birds weighed >150 g, we fitted them with a necklace-style transmitter (American Wildlife Enterprises, Monticello, FL) weighing 6.5–6.9 g (4.3–4.6% of body mass; Brander and Cochran 1969). After radiomarking, we released individual bobwhites at the site of capture. Researchers at RPQRR conducted the trapping, radiomarking, and tracking of bobwhites for general bobwhite ecology research. We conducted the experimental trials reported in this manuscript under Texas Tech University Animal Use Protocol No. 07051-08.

From December 2009–March 2010 and November 2010–March 2011, we used a truck-mounted omnidirectional antenna attached to an R2000 type receiver (Advanced Telemetry Systems, Ashanti, MN) to find approximate locations of coveys with ≥1 radio-marked member. Once we found an approximate location, we switched to a hand-held Yagi antenna to home in on the covey's exact location. Prior to homing, we recorded wind speed, temperature, and time of day. One to 3 remote observers deployed to higher points on the surrounding landscape with encompassing views of the area to aid in data collection. Once the remote observer(s) arrived in place, we initiated the treatment. Each treatment used different criteria (described below), but all followed the primary format of homing to the covey on foot until the birds flushed.

Once the covey flushed, the remote observer(s) recorded the time of the flight from flush to land and noted the location at which the birds landed. If birds landed out of sight of the remote observer(s), we relocated them with telemetry. We attempted to relocate the birds as quickly as possible to find their landing point and not the point to which they moved after landing. We do not have a record of which flushes the observer(s) missed the landing, but we estimate this occurred in fewer than 20% of all flights. When a bird landed after being chased by the avian threat, however, the raptor remained with the bobwhite until we reached the landing spot. The observer(s) witnessed this on >30 occasions and we assume this occurred when the observer(s) did not witness the landing. We measured the distance from the threat to the point of flush with a laser range finder

(Yardage Pro Sport 450; Bushnell, Overland Park, KS). We recorded flushing strategy (if all flush at once, or in partial flushes), making special note of which subsequent flush the radio-marked bird joined. We used a handheld global positioning unit (Garmin GPS Map 60CSxl; Garmin, Olathe, KS) to record the coordinates of flush point and landing or re-location point. We determined the precise times of trials by the availability of volunteer assistance. After data collection in the field, we used MapSource[®] software to measure distances of individual bobwhite flights; we divided the distances for individual flights (m) by the respective times of flights (seconds) to estimate flight speed.

Not all flushes provided complete sets of data because we took multiple measurements for each flushing and flight event. For example, the remote observer was not always capable of seeing where the bobwhite landed and a stopwatch malfunction or an observer error would prevent estimation of the flight speed. We did not discount these trials; rather, we used the portions that were available for each measurement in reference to overall flight distance or cover use. Thus, many of the sample sizes were not identical within threat types. For example, the sample size for flight distance of raptor-flushed bobwhites did not equal the sample size for flight speed of raptor-flushed bobwhites because we obtained a start and stop location for all flights but did not always obtain a time for the entire flight. For all measurements, we report means and standard deviations. For all model estimates, we report model-averaged parameter estimates (standardized and un-standardized) and unconditional standard errors.

Flush Treatments

We included a researcher treatment to mimic a researcher monitoring radio-marked quail via homing. During this treatment only the data collector and radio-telemetry operator homed in on the covey until it flushed. We conducted these trials during the daylight hours 0900 to 1800.

We designed a hunter treatment to replicate a quail hunting scenario. The radio-telemetry operator homed in on coveys accompanied with a hunting party that included a dog and shotgun handler, as well as the data recorder with 1–3 hunting party members. When at an estimated distance of 40 m from the covey, the handler sent the trained quail-hunting dog to pinpoint the covey. Once the dog pointed the covey, we continued the hunting scenario with the hunting party walking together to the area the dog pointed and flushing the birds. The dog handler then fired 2 blank rounds from a shotgun as bobwhites flushed. We conducted these trials during the daylight hours 0900 to 1800.

We designed a raptor treatment to replicate a predation attempt by an accipitrine hawk. A radio-telemetry operator homed in on a covey along with the data collector and an experienced falconer. The falconer held a trained northern goshawk (*Accipiter gentilis*) on his fist. The falconer released the goshawk the moment a bobwhite (or covey) flushed. The individual bobwhite that the goshawk chased was the bird

from which we collected flight and cover use data. In this treatment, the initial threat perceived by the bobwhite may have been terrestrial; however, once the goshawk gave chase, the bobwhite's main threat was certainly the raptor. We conducted these trials during the daylight hours 0900 to 1900.

Unlike the 3 previous threats, which are mostly or exclusively diurnal threats, predation by mammalian carnivores (e.g., bobcats [*Lynx rufus*] or coyotes [*Canis latrans*]), occurs during both diurnal and nocturnal or crepuscular hours (Laundré and Hernández 2003, Donovan et al. 2011). We chose to simulate nocturnal mammalian predatory events because recreating diurnal mammalian predatory events was logistically limiting. We conducted these flushes closer to dawn than dusk to lessen the time of roosting disturbance in cold temperatures. Because bobcats and coyotes hunt by stealth, we simulated their entrance on bobwhites with a single observer walking silently to the bobwhite's location. The observer wore headphones to listen for the transmitter signal from a hand-held receiver and Yagi antenna so the bobwhites would not hear the beeps emitted from the receiver. The observer slowly homed in on the covey without using any lights. Following this protocol, we presented the bobwhites with a terrestrial threat at night that made no noise other than the sounds of walking. The remote observer watched through a forward looking infrared (FLIR) thermal imaging scope (model L-3 thermal-eye palm IR 250; Raytheon, Waltham, MA), which allowed for a continuous view of the entire flight and recording of data consistent with daytime flushes. Following the flush, we recorded coordinates and flagged the bobwhite's flushing and landing points. We revisited each point during daylight hours to record vegetation data.

To reduce bias from habituation to the researcher and threat type, we staggered the flushing of individual coveys. Because the membership within a covey is not static (e.g., individuals die, coveys split or merge) we recognize that dividing sample effort by covey is not truly standardized, but it was the only logistically feasible approach. Although our assumption of consistent covey membership is not true, it was the best option we had to standardize our data collection. We flushed each covey with each threat only once in the beginning of the hunting season (Nov–Dec) and once at the end of the hunting season (Feb–Mar). We did not flush coveys more than once within the same week. We assigned the order of treatment given logistical constraints of completing each treatment (i.e., availability of falconer, dog handler and hunter, or thermal imaging scope). We were unable to complete the mammalian flushes until the last month of the study.

Vegetation Measurement

For each treatment trial, we measured visual obstruction, shrub intercept, and angle of obstruction using a modification of the methods described by Kopp et al. (1998) to include cover available during flight as well as at flushing and landing points. We did not assume that any point on the landscape was available for bobwhites once they had flushed

from a threat in the manner of Kopp et al. (1998); instead we compared each landing site to a point along its corresponding flight path. We sampled points at flushing and landing points. We sampled another point along the flight path at a randomly selected distance from the flushing point and then moved a random distance (up to 20 m) on a right angle from the center of the path (Fig. 1). We recognized that a covey or a single bird will fly a minimum distance once flushed. To avoid sampling an area that was not available to the quail because it was too close to the flushing point, we did not include points within 20 m of the flushing point.

To sample visual obstruction, shrub intercept, and angle of obstruction, we positioned 8, 4.0-m transects originating from the center of each point and following the cardinal and intercardinal directions (Kopp et al. 1998). We used a Robel pole with a diameter of 2.54 cm and painted vertical intervals of 10 cm, viewed from a distance of 4 m and height of 1 m, to measure visual obstruction height of vegetation <1.0 m tall. We measured shrub intercept along each transect. Each point measured could have a total shrub cover of 3,200 cm and we present shrub intercept as percent intercept of the 3,200 cm. To estimate the angle of obstruction, we pointed a

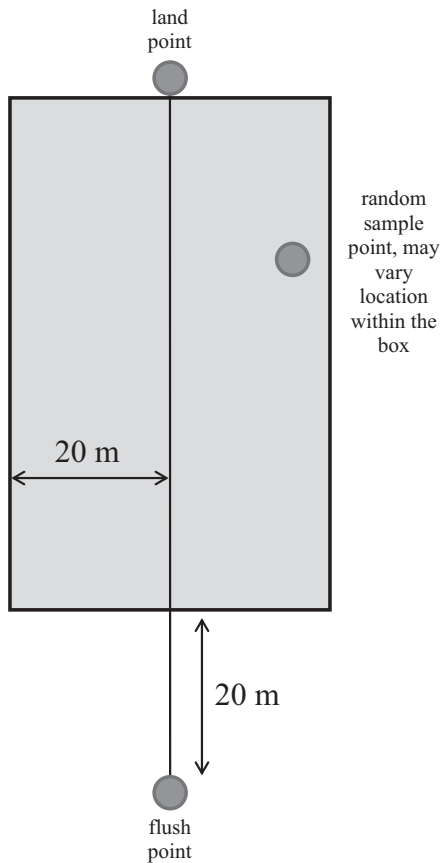


Figure 1. A depiction of the 3 vegetation sampling points along a bobwhite's flight path at the Rolling Plains Quail Research Ranch, Fisher County, Texas, collected from December 2009–April 2011. The box contains the random sample point for the flight. The location of the random point could be anywhere within the box and was pre-determined by a coin flip for left or right and a random number list for distance along the flight path and distance horizontal to the flight path.

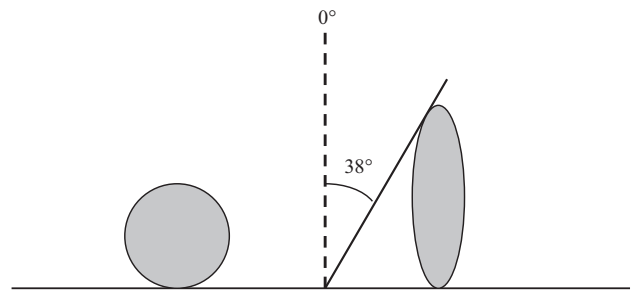


Figure 2. A depiction of the sampling method for angle of obstruction at the Rolling Plains Quail Research Ranch, Fisher County, Texas, collected from December 2009–April 2011. The center of the point is shown where the vertical and horizontal lines intersect. The circular shapes represent woody vegetation within 4 m of the point's center. We measured the angles such that straight up was 0° and horizontal on the ground was 90°.

Robel pole with an attached carpenter's level from the center point of the sampling area to the nearest non-grass vegetation along each of the transects and recorded the angle (Fig. 2; Harrell and Fuhlendorf 2002).

Statistical Analysis

We selected 6 of the same a priori predictor variables for both flight distance and flight speed. These were 1) treatment type (i.e., researcher, hunter, raptor, or mammal); 2) date, the day within the hunting season starting with 1 October being day 1 and ending with 31 March as day 182; 3) time of day; 4) wind speed; 5) distance to flush, the distance between the observer and bobwhite at time of flush; and 6) covey size. We added the variable shrub intercept, which was the intercept of woody cover at a random point along the flight path, to the global model for estimating flight distance; however, we did not think this variable would be influential for estimating flight speed.

We ran model selection with the MASS package (Venables and Ripley 2002) in program R (R Development Core Team 2011). We used a step-wise regression performed backwards instead of a priori models because we did not predict any specific combination of variables to be important. The package MASS removed variables from the global model until the ΔAIC_c value decreased by <2. We averaged parameters over the entire model set using corrected Akaike's Information Criterion (AIC_c) weights for each model (Anderson 2008). We created 2 model-averaged equations, 1 with raw data and 1 with standardized data, for both flight distance and flight speed. The first equation can be used for predictive purposes, the second allowed us to compare our parameters directly to identify which variables held the most influence in predicting flight distance and flight speed.

To examine bobwhite's selection for visual obstruction, shrub intercept, and angle of obstruction at landing sites, we compared data from landing points to data from random points along flight paths among individual treatments. Because the data on visual obstruction did not meet the assumptions of normality or homogeneity of variances, we used a pairwise Wilcoxon signed rank test to test for differences between the landing and random points. To

estimate shrub use on a species level, we used a Chi-square test of independence to compare frequencies among the shrub species at random and landing points within each treatment type. We combined shrub species that were available fewer than 4 times at random points into a cumulative category labeled other. This varied among treatments, and thus not all data sets have the same categories of shrubs. We also compared the cover-use measurements (visual height obstruction, shrub intercept, and angle of obstruction) of diurnal flush locations to nocturnal flush locations to assess differences between the diurnal locations and the roosting sites. We combined all 3 diurnal treatment types (researcher, hunter, and raptor) together and conducted a Wilcoxon rank sum test to compare the 2 categories.

Flushing data did not meet assumptions of normality, so we analyzed the relationship of covey size and distance to flush with a Spearman rank correlation rho test. We looked for a flushing strategy of marked birds by dividing the flushes into 2 groups: 1) birds that flew on the first flush, and 2) birds that flushed on the second or later flush. For analysis, we removed all flushes with only a single bird present. Using the package aod (Lesnoff and Lancelot 2010), we ran a Wald's Chi-squared test on the treatment-flushing matrix to assess the significance of treatment type on flushing of the radio-marked bird.

RESULTS

We conducted 72 trials of the researcher treatment, 50 of the hunter treatment, and 75 of the raptor treatment between 0821 and 1800 hours. Restricted availability of the FLIR thermal imaging scope limited us to only 25 trials of the mammalian (e.g., nocturnal) treatment conducted between the hours 0203 and 0611 hours.

Flight Distance

For analysis of flight distances by treatment type, we obtained 66 usable data sets for the researcher treatment, 45 for the hunter treatment, 57 for the raptor treatment, and 24 for the mammalian treatment, for a total of 192 bobwhite flights. We observed the average distance of all flights at

157.4 ± 71.5 m. The highest ranked model included the variables treatment type and covey size (Table 1) and held 42.6% of the weight of all models. Over 90% of the weight of all models was held in the 3 top models. Through model averaging of standardized beta estimates, we found treatment type to be the primary predictive variable, followed by covey size (Table 2). The intercept accounted for expected flight distance resulting from researcher threat. The hunter and raptor threats increased the expected flight distance by 36.0 ± 13.1 m and 33.5 ± 12.3 m, respectively. The mammalian threat decreased the expected distance flown by 46.0 ± 16.4 m. Covey size positively influenced the expected flight distance by an estimated 2.4 ± 1.23 m for each bird within the covey.

Flight Speed

For analysis of flight speed among treatment types, we obtained 21 usable samples for researcher threat, 21 for hunter threat, 25 for raptor threat, and 10 for mammalian threat, for a total of 77 estimates of flight speed at an average of 15.1 ± 4.9 m/s. The highest ranked model contained the variables treatment type, time of day, and distance to flush (Table 3), which held 56% of the weight for the model set. Over 90% of the weight for the model set was held by the top 3 models. The model-averaged standardized beta estimates indicated treatment as the primary predictor variable for flight speed, with time of day and distance to flush appearing to have little to no real impact on flight speed (Table 4). The intercept accounted for expected flight speed resulting from researcher threat, which is slightly increased (0.6 ± 1.4 m/s) by the hunter threat. The mammalian threat increased expected flight speed by 1.7 ± 1.6 m/s, and the raptor threat increased expected flight speed the most of all treatments by 3.1 ± 1.4 m/s.

Cover Selection

Bobwhites selected landing points with greater visual obstruction than what was randomly available on the escape flight path when threatened with the hunting treatment and the raptor treatment (Table 5). When flushed by the hunter treatment and raptor treatment, bobwhites landed in areas with a median vegetation height 6.2 cm taller (95% CI for difference = 0.6, 12.5 cm, $n = 41$, $Z = -2.11$, $P = 0.034$) and

Table 1. Models obtained through stepwise regression providing the best predictors of bobwhite flight distances at the Rolling Plains Quail Research Ranch, Fisher County, Texas, during the winter months of December 2009–March 2011 with the predictor variables treatment (flushed by researcher, hunter, raptor, or mammal), covey size, wind speed (wind), shrub intercept at landing point (shrub), time of day (time), date of trial (date), and distance to flush (distance), and an intercept-only model.

Model	K^a	AIC _c ^b	Δ_i^c	w_i^d	R^2
Treatment, covey size	3	1,618.74	0.00	0.426	0.145
Treatment, covey size, wind	4	1,619.26	0.52	0.329	
Treatment, covey size, wind, shrub	5	1,620.72	1.98	0.158	
Treatment, covey size, wind, shrub, time	6	1,622.69	3.95	0.059	
Treatment, covey size, wind, shrub, time, date	7	1,624.76	6.02	0.021	
Treatment, covey size, wind, shrub, time, date, distance	8	1,626.91	8.17	0.007	
Intercept	1	1,640.71	21.96	0.000	

^a Number of variables.

^b Akaike's Information Criterion corrected for small sample size.

^c Difference in AIC_c values between current model and model with lowest AIC_c value.

^d Akaike weights.

Table 2. Model-averaged non-standardized parameter estimates ($\hat{\beta}$) and model-averaged standardized parameter estimates $\hat{\beta}_s$ associated unconditional standard errors (SE) for the models predicting bobwhite flight distances (m) at the Rolling Plains Quail Research Ranch, Fisher County, Texas, during the winter months of December 2009–March 2011 with the predictor variables treatment (intercept [researcher], hunter, raptor, or mammal), covey size, wind speed (wind), shrub intercept at landing point (shrub), time of day (time), date of trial (date), and distance to flush (distance).

Variables	$\hat{A}\hat{\beta}$	SE	$\hat{A}\hat{\beta}_{s,As}$	SE
Intercept	126.32	15.77	141.77	11.61
Hunter	36.02	13.13	36.02	13.13
Raptor	33.53	12.31	33.53	12.31
Mammal	-46.00	16.43	-46.00	16.68
Covey size	2.42	1.23	9.69	4.93
Wind	0.80	1.29	3.48	5.63
Shrub	-0.00	0.01	-0.94	5.70
Time	-0.00	0.02	-0.22	7.57
Date	0.00	0.16	0.03	5.69
Distance	0.00	0.62	0.00	5.32

38.1 cm taller (CI = 28.8, 47.5 cm, $n = 34$, $Z = -4.91$, $P < 0.001$), respectively, than was randomly available.

During raptor trials, bobwhites selected for landing points with a median shrub intercept proportion 42.2% greater (CI = 32.4, 51%) than at random sites ($n = 53$, $Z = -5.52$, $P < 0.001$; Table 5). At these landing sites the average shrub intercept across 8 m was 451.5 cm \pm 240.1. However, bobwhites exhibited no selection for shrub cover during trials of the researcher-, hunter-, or mammal-threat treatments. We observed a similar pattern when examining the average angle of obstruction at landing points among the treatments; only after undergoing the raptor treatment did the bobwhites select a lower (49.8, $n = 35$, $Z = 4.69$, $P < 0.001$) average angle of obstruction (implying a smaller amount of sky visible) at landing points than was randomly available along the flight path. Bobwhites flushed by the raptor treatment selected landing areas with a median angle of obstruction 70.4° lower (CI = 52.9, 81.2) than at random sites along the flight path.

The study area had a diverse community of woody vegetation. Bobwhites exposed to researcher and mammal treatments did not select for any particular shrub cover for landing sites. However, shrub cover composition at landing points differed from what was along the flight paths within the hunter ($X^2_2 = 45.5$, $P < 0.001$) and raptor treatments

($X^2_{12} = 98.3$, $P < 0.001$). When presented with hunter or raptor threats, catclaw mimosa comprised 42.5% and 27.8% of the woody vegetation contained within the random locations on bobwhites' flight, respectively, but only comprised 26.2% and 4.3% of the woody vegetation at respective landing points. Within the raptor trials, bobwhites selected for dense woody shrubs or mottes of shrubs (Table 5). Although our data were insufficient for statistical analysis of proportionality of these species at random and landing sites, we noticed increased usage of sturdier shrubs including species such as agarita, hackberry, and littleleaf sumac, and for mottes of Englemann's prickly pear. For a detailed list of vegetation use see Perkins (2012). We recorded 56 trials in which bobwhites escaped from the goshawk by going to ground cover; bobwhites used underground refugia (e.g., animal burrows) in 15 (26.8%) of these trials.

We also found a significant difference in vegetation composition and structure between diurnal and nocturnal locations (Table 6). The average visual height obstruction at nocturnal locations was 7.3 cm lower than diurnal locations ($n = 138$, $W = 1,694.5$, $P = 0.03$), shrub intercept at nocturnal locations averaged 10.1% lower than diurnal locations ($n = 185$, $W = 2,413$, $P = 0.02$), and angles of obstruction averaged 18.5° higher than diurnal locations ($n = 137$, $W = 834.5$, $P = 0.005$).

Flushing Behavior

We detected a positive correlation of covey size and distance to flush in both years of the study (2009–2010 $n = 40$, $r = 0.36$, $S = 6,807.55$, $P < 0.022$, and 2010–2011 $n = 145$, $r = 0.47$, $S = 263,827.1$, $P < 0.001$) and when the years were pooled ($n = 186$, $r = 0.44$, $S = 584,845.8$, $P < 0.001$). However, we did not detect any difference of flushing strategy (i.e., the timing of a bird's flush in relation to sub-flushes of the covey) of radio-marked quail among treatment types ($n = 108$, $X^2_3 = 0.24$, $P = 0.97$).

DISCUSSION

We found threat type influenced escape behavior of bobwhites in our study. Bobwhites flushed during raptor and hunter trials flew farther than those flushed with a researcher threat. Bobwhites that were flushed at night flew a shorter distance than the other 3 threat types. We reason

Table 3. Models obtained through stepwise regression providing the best predictors of bobwhite flight speed at the Rolling Plains Quail Research Ranch, Fisher County, Texas, during the winter months of December 2009–March 2011 with the predictor variables distance to flush (distance) covey size, time of day (time), wind speed (wind), date of trial (date), and treatment (flushed by researcher, hunter, raptor, or mammal), and an intercept-only model.

Model ¹	K^a	AIC _c ^b	Δ_i^c	w_i^d	R^2
Treatment, time, distance	4	239.38	0.00	0.56	0.194
Treatment, time, distance, wind	5	240.77	1.39	0.27	
Treatment, time, distance, wind, covey size	6	242.41	3.04	0.11	
Treatment, time, distance, wind, covey size, date	7	244.73	5.35	0.03	
Intercept	1	245.67	6.29	0.03	

^a Number of variables.

^b Akaike's Information Criterion corrected for small sample size.

^c Difference in AIC_c values between current model and model with lowest AIC_c value.

^d Akaike weights.

Table 4. Model-averaged non-standardized parameter estimates ($\hat{\beta}$) and model-averaged standardized parameter estimates $\hat{\beta}_s$ and associated unconditional standard errors (SE) for the model to predict bobwhite flight speed (m/s) at the Rolling Plains Quail Research Ranch, Fisher County, Texas, during the winter months of December 2009–March 2011 with the predictor variables treatment (intercept [researcher], hunter, raptor, or mammal), covey size, wind speed (wind), time of day (time), date of trial (date), and distance to flush (distance).

Variables	$\hat{\beta}$	SE	$\hat{\beta}_s$	SE _s
Intercept	10.66	3.08	13.67	1.03
Hunter	0.60	1.43	0.60	1.43
Raptor	3.12	1.37	3.12	1.37
Mammal	1.65	1.56	1.65	2.40
Covey size	0.02	0.16	0.07	0.65
Wind	-0.05	0.14	-0.21	0.62
Time	0.00	0.00	1.16	0.79
Date	0.00	0.01	0.00	0.62
Distance	-0.11	0.05	-1.23	0.54

that both the aerial threat and the gun's report during the raptor and hunter threats, respectively, provided increased impetus to escape once the bobwhites were already in flight. In contrast, once flushed by the researcher, no follow-up threat occurred and the escape flight was shorter. Finally, bobwhites' nocturnal visual capabilities may be poor and could render flying at night a dangerous endeavor. Colliding with a solid object or being impaled on shrub or tree branches are legitimate threats and potential causes of injury or death for bobwhites. Thus flying at night is an activity that appears to be limited to only the extent necessary. Our mean flight distance was 110.4 and 97.1 m longer than the findings of Kassinis and Guthery (1996) and Perez et al. (2002), respectively. We attribute these discrepancies to

methodological differences, as well as differences in location of study areas. Kassinis and Guthery (1996) flushed bobwhites from vehicles or while walking, whereas Perez et al. (2002) used a radar gun to record flight speeds of birds released from capture bags and then estimated the distances flown based on the speed recorded and the time of the flight. Kassinis and Guthery, as well as Perez et al. studied in the South Texas Plains and Coastal Plains ecoregions of Texas, and our study took place in the Rolling Plains ecoregion of Texas.

Within flight speed beta estimates, treatment type proved most influential when predicting flight speed, primarily for the increase in speed related to the raptor threat. We expected models with the raptor treatment to predict the fastest flight speeds based upon our observations of bobwhites chased by raptors. While gathering data for this study we observed bobwhites fly an arced flight path when flushed by the researcher, hunter, and mammal threats. This flight consisted of an acceleration period to the height of the flight and a deceleration period during which the bobwhite would no longer flap but would instead set their wings while gliding in to land. During raptor trials, bobwhites displayed no visually detectable deceleration phase and thus should logically have been flying at a top speed for longer periods. Although we could not quantify it, we also observed the paths bobwhites traveled during the raptor-induced flights to have a greater degree of tortuosity than the flight paths from terrestrial threats (i.e., the remaining 3 treatments including the mammal threat viewed through the thermal imaging technology). However, our flight speed estimates were derived by dividing distance of the flight by total time of the flight, assuming a straight line

Table 5. Means and standard deviations of visual obstruction, shrub intercept, and angle of obstruction at random and landing points for treatments (flushed by researcher, hunter, raptor, or mammal) at the Rolling Plains Quail Research Ranch, Fisher County, Texas, during the winter months of December 2009–March 2011. An * denotes significant difference ($P < 0.05$) between the means at the random and landing points within the treatment category based on a Wilcoxon signed rank test. Shrub intercept is presented as a percentage of total area sampled—a possible 3,200 cm (i.e., if a point had 640 cm of shrub intercept then it would be presented as 20%).

Vegetation measurement	Researcher	<i>n</i>	Hunter	<i>n</i>	Raptor	<i>n</i>	Mammal	<i>n</i>
Visual obstruction (cm)								
Random	34.8 ± 16.2	40	30.5 ± 14.7	41	30.0 ± 14.7	34	30.7 ± 19.4	23
Land	35.2 ± 15.2		39.0 ± 19.6*		66.6 ± 20.5*		29.6 ± 8.0	
Shrub intercept (%)								
Random	14.1 ± 21.6	62	15.5 ± 23.7	45	19.2 ± 25.5	53	10.5 ± 17.4	23
Land	16.0 ± 17.6		15.8 ± 22.6		56.4 ± 30.0*		6.6 ± 10.7	
Angle of obstruction (°)								
Random	70.6 ± 29.7	40	71.9 ± 29.4	41	62.2 ± 37.0	35	71.1 ± 32.0	23
Land	65.7 ± 32.6		70.0 ± 31.3		12.4 ± 25.8*		80.6 ± 20.8	

Table 6. Means and standard deviations of vegetation height obstruction, shrub intercept, and angle of obstruction at diurnal (researcher, hunter, and raptor treatments) and roosting (mammal treatment) flushing points at the Rolling Plains Quail Research Ranch, Fisher County, Texas, during the winter months of December 2009–March 2011. An * denotes significant difference ($P < 0.05$) between the means at the random and landing points within the treatment category based on a Wilcoxon signed rank test. Shrub intercept is presented as a percentage of total area sampled—a possible 3,200 cm (i.e., if a point had 640 cm of shrub intercept then it would be presented as 20%).

Vegetation measurement	Diurnal	<i>n</i>	Roosting	<i>n</i>
Vegetation height (cm)	36.07 ± 14.77	115	28.75 ± 11.79*	23
Shrub intercept (%)	13.93 ± 19.54	162	3.88 ± 6.04*	23
Angle of obstruction (°)	67.62 ± 31.25	114	86.13 ± 6.95*	23

between the flushing and landing point. Thus, the parameter estimate we found for the raptor treatment may be biased low.

Covey size also was positively related with flight distance. We speculate that a covey will fly until all members, or perhaps a lead bird of the covey feels it is safe to land. Thus with more members of the covey, a particular bird likely requires a longer distance between the flushing point and landing point to feel secure. An alternative cause for the correlation would be the selfish herd theory in which individuals in groups may attempt to put the other group individuals between themselves and the threat (Hamilton 1971). This may translate to larger groups flying farther than smaller groups or single birds.

When investigating cover use, we observed that bobwhites select different forms of escape cover according to specific threat types. Our results indicate primarily a difference in response to terrestrial or aerial threats. This threat-specific behavior dependent upon predator hunting mechanism has been documented with lesser prairie-chickens (Behney et al. 2011) and redshanks (Cresswell 1996) responding differently depending on raptor species, and with mallard ducklings that were observed to display alternative behaviors for avian, terrestrial, and aquatic predators (Dessborn et al. 2012).

Bobwhites pursued by a raptor likely seek dense landing cover for protection (Guthery 2000:10). Why hunter-flushed bobwhites selected for landing points with taller visual obstruction is not clear, but the aural threat stimulus of the gun blasts while in flight may increase the urge to find greater amounts of cover. Alternatively, the influence of the hunting dog during the hunter scenario could incite the bobwhites to find higher cover. During hunter trials, bobwhites selected for taller visual obstruction but not denser shrub cover, implying that landing in shrubs is not preferred and is reserved for situations where danger is imminent (i.e., an avian predator giving chase). Bobwhites may risk blunt-force trauma or impalement when landing in dense, woody shrubs at high speeds, and such escapes may be acts of desperation due to imminent threat. In this study, we also observed bobwhites using underground refugia to escape from the threat of a raptor. Although falconers have observed quail escape into burrows when pursued by trained raptors (C. Boal, U.S. Geological Survey, unpublished data), we believe this is the first quantitative documentation of bobwhites using burrows or subterranean cover. However, this escape behavior may have unidentified risks. Many radio transmitters placed on bobwhites at the RPQRR are relocated later in burrows under shrubs (B. Koennecke, Rolling Plains Quail Research Ranch, personal communication). Whether these transmitters were recovered and brought to the burrows by rodents (e.g., *Neotoma* spp.) or are from bobwhites that took refuge in burrows and were killed in the burrows by other animals remains unknown. Further research is necessary to assess the potential dangers bobwhites may incur when using this escape tactic.

We found bobwhites selected roosting locations with little vegetative cover. Because understanding roosting coverts was

not an initial objective for this study, we did not collect random locations within the landscape to compare to the nocturnal locations at which we found bobwhites. However, our findings are consistent with the findings of similar conditions at bobwhite roosting sites by Klimstra and Ziccardi (1963) and Hiller and Guthery (2005) where bobwhites were observed to roost in sparsely vegetated areas. Tillman (2009) studied nocturnal roosting and anti-predation behavior of gray partridges (*Perdix perdix*) and reasoned that choosing exposed roosting locations was a form of predator avoidance behavior that highlighted the importance of unobstructed clear flight paths for escape if approached by a predator. We suspect Tillman's (2009) theory of required escape routes applies similarly to bobwhite roosting sites.

Our findings also support Tillman (2009) in that larger coveys flushed farther from a threat than smaller coveys. However, we disagree with Tillman's reasoning. He concluded that the partridges had difficulty recognizing the presence of the threat from afar and would thus not flush until the threat was close enough to be recognized. Tillman (2009) reasoned that Lima's (1995) theory applied and that with the many eyes and ears of a large covey, the partridges were more likely to recognize the threat from farther away and flush accordingly. We presume all bobwhites in the covey being approached were aware of our advance. We submit that bobwhites hide or hold tight rather than flush when faced by danger, and they flush only when hiding is no longer a viable option. A larger group will have a greater chance of having an individual bird with a low threshold for flushing instead of hiding. Once a single bird has flushed, thus compromising the remaining bobwhites' location, the remaining birds are then motivated to fly as well. This is possibly a factor of age—older, experienced birds may hold tight longer, whereas younger birds may flush earlier and larger coveys typically have more young birds. Alternatively, Williams et al. (2003) found that bobwhites select for covey sizes of 11 birds. Their study found that large coveys have high mortality but they speculate that the dilution effect hypothesized by Krebs and Davies (1993) entices birds to select for larger coveys because their individual chances of being selected by a predator are lower. Thus, coveys with more individuals may flush with less harassment (i.e., from farther away) because the individuals within the covey feel safer than those in a covey with fewer individuals.

MANAGEMENT IMPLICATIONS

Based on our data, we suggest a patchwork landscape similar to previously listed management recommendations (e.g., Guthery 2000:92–96) would benefit bobwhites in avoiding predation. Specifically, our data highlight the importance of dense woody coverts for escape from raptor threats, as well as open areas, even with patches of bare ground, for roost sites to facilitate threat-avoidance in nocturnal situations. We also observed bobwhites landing in woody coverts that contain Englemann's prickly pear ($n = 32$). Thus we caution against complete cacti removal, a popular trend on hunting ranches, because the practice may prove detrimental for bobwhites

seeking refuge. Given that the average flight distance we observed was 157 m (CI = 147.3, 167.5) across all threat types, we suggest the landscape be managed so that no point is farther than approximately 150 m from a dense woody covert. In conjunction with Guthery's (1999) slack hypothesis, however, the relevancy of our findings is limited to the Rolling Plains ecoregion within Texas and of course subject to natural variability within the landscape. The mottes, or dense woody coverts, of shrubs we observed bobwhites using to escape raptors were comprised of a variety of species. What was consistent, however, was that the mottes often included a multitude of woody species that grew together, creating a dense cover from the ground to >1.0 m and with an average diameter of 4.4 m. Continued research focused on understanding the use, risks, and values of subterranean refugia as bobwhite escape cover may enhance our ability to manage and conserve bobwhites. Additionally, a better understanding of the importance of woody cover, in terms of both configuration and dispersion, will facilitate habitat management efforts for the species. However, we stress that we conducted our study in a very specific location and vegetation community. Our findings may not be applicable across other vegetation communities within the species distribution but provide insights as to new avenues of research that may be applied elsewhere.

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