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Original Article

Nocturnal Movements and Habitat Selection of Mesopredators Encountering Bobwhite Nests

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ABSTRACT Northern bobwhites (*Colinus virginianus*) represent a valuable resource for upland game-bird hunters and the rural economies they support; however, bobwhite populations are declining across the United States. As ground-nesting birds, bobwhites are highly susceptible to mammalian predation during the breeding season. We placed global positioning collars on 6 coyotes (*Canis latrans*), 4 bobcats (*Lynx rufus*), and 11 raccoons (*Procyon lotor*) in Texas, USA, during the nesting season of bobwhites (April–August of 2009–2011) to assess their habitat selection and use, as well as determine the relative frequency with which they may encounter bobwhite nests. Overall, nightly encounter rate of predators with known bobwhite nest sites was low. Coyotes encountered nest sites 3 times more frequently than male raccoons and 7 times more frequently than bobcats. Female raccoons did not come within 50 m of any nest locations. The higher encounter rate of coyotes with bobwhite nest sites was associated with the similarity of habitat preference of coyotes and bobwhites for grasslands and grass–shrub habitats and the wide-ranging nocturnal paths of coyotes. Bobcats and raccoons had shorter nightly paths and mainly used habitats providing a greater degree of cover than is typically suitable for nesting bobwhites. Male raccoons were more mobile than females and made greater use of the grass–shrub habitat, and thus were more likely to encounter quail nests. Despite having lower individual encounter rates with bobwhite nest sites than did coyotes, male raccoons remain important predators of quail nests because they have the behavioral ability to attain greater population densities than those of the more territorial coyotes and bobcats.

KEY WORDS animal movements, bobcat, coyote, GPS, habitat selection, northern bobwhite, predation, raccoon, Rolling Plains, Texas.

Predation is the primary cause of mortality at all stages of the northern bobwhite's (*Colinus virginianus*) life cycle (Rollins and Carroll 2001, Rader et al. 2007). Habitat loss and fragmentation have been identified as the ultimate causes of the ongoing decline in abundance of both bobwhites and scaled quail (*Callipepla squamata*; Brennan 1991, Veech 2006, Hernández et al. 2013). However, these landscape-level changes can alter the balance of predators and prey, potentially exacerbating predation impacts at the local scale (Crooks and Soulé 1999, Crooks 2002). Interactions between habitat fragmentation and predators are spatially complex (Schneider 2001), but with increasing habitat loss for the prey species the effects of predation tend to increase, particularly when predators are habitat generalists (Ryall and Fahrig 2006). Over the past 30 years there has been ongoing concern that an increase in abundance of mesopredators (i.e., small to medium-sized mammalian predators weighing <15 kg; Roemer et al. 2009), may be having significant negative impacts on a wide variety of wildlife species (Prugh et al. 2009). These mammals tend to be the main predators of quail and their eggs in the summer breeding season, whereas in winter avian predation becomes more important (Burger et al. 1995).

Predator removal to improve the nesting success of quail is a common management practice but has had limited success in increasing quail population densities (Guthery and Beasom 1977, Rader et al. 2011). Reduction in one species of predator often leaves more food available for the next (Henke and Bryant 1999, Roemer et al. 2009); thus, predator "reduction" often becomes predator "replacement." Nevertheless, even predator replacement may impact quail population recruitment rates, because not all predators constitute equal threats to quail; the problem lies in identifying which predator species have more detrimental effects on quail populations and which may be comparatively less problematic. We approached the problem by placing global positioning system (GPS) collars on coyotes (*Canis*

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latrans), bobcats (*Lynx rufus*), and raccoons (*Procyon lotor*) to assess the relative threat each species posed to nesting bobwhites in the grassland habitat of the Rolling Plains of Texas, USA. Coyotes are common nest predators for bobwhites in South Texas (Rader et al. 2007) and bobcats and raccoons have been documented as nest predators in West Texas (Hernández et al. 1997). We estimated the frequency with which each species was likely to encounter known bobwhite nest sites and how this threat may be influenced by the social organization, habitat use, and mobility of each species.

STUDY AREA

We conducted our study on the 1,910 ha Rolling Plains Quail Research Ranch (RPQRR) in Fisher County, Texas, during the months of April–August of 2009–2011, to coincide with the nesting season of northern bobwhites, as well as other grassland-nesting bird species. The Rolling Plains ecological region was part of the southern extension of the Great Plains (Wright and Bailey 1982). Historically this region supported abundant populations of bobwhite and scaled quail and hunting remains both culturally and economically important despite declines in abundance (Rollins 2007). The climate of the region was semi-arid; average temperatures ranged from -2° C to 13° C in January and 21° C to 36° C in July (Bomar 2011). Long-term annual precipitation was 574 ± 152 mm with peak precipitation in May and September (National Oceanic and Atmospheric Administration [NOAA] 2012).

Topography of the region was gently rolling plains dissected by narrow stream valleys and a few rocky outcroppings. Originally, the vegetation was tall and mid-grass prairie, but much of the land was cleared for agriculture, principally non-irrigated cotton and wheat. Although surrounded by cropland to the north and east, and mesquite (*Prosopis glandulosa*)-dominated rangeland to the south and west, the vegetation on the RQPRR was predominantly native grassland with scattered shrubs and cacti (*Opuntia* spp.) on clay loam, loamy prairie, sandy loam, and shallow ecological sites (Soil Survey Geographic Database [SSURGO] 2009). Shrub density was greatest on the sandy loam ecological sites surrounding the flat-topped rocky ridge (very shallow ecological site) that covered 9% of the area and ran north–south through the center of the property. Tumbled sandstone slabs and dense shrubs along the sides of the ridge provided good cover for mesopredators. A further 11% of the land was classified as loamy bottomland ecological site associated with drainages and an ephemeral creek system that supported a strip of riparian woodland with taller trees (Fig. 1).

The RPQRR was managed specifically as a research and demonstration site to enhance populations of bobwhites. Cattle grazing was restricted to the far northeastern and southwestern pastures and a low net-wire fence bounded the property. Supplemental feed in the form of milo (*Sorghum bicolor*) or pelleted feed was provided for the quail in 42-barrel feeders distributed throughout the ranch. No predators were

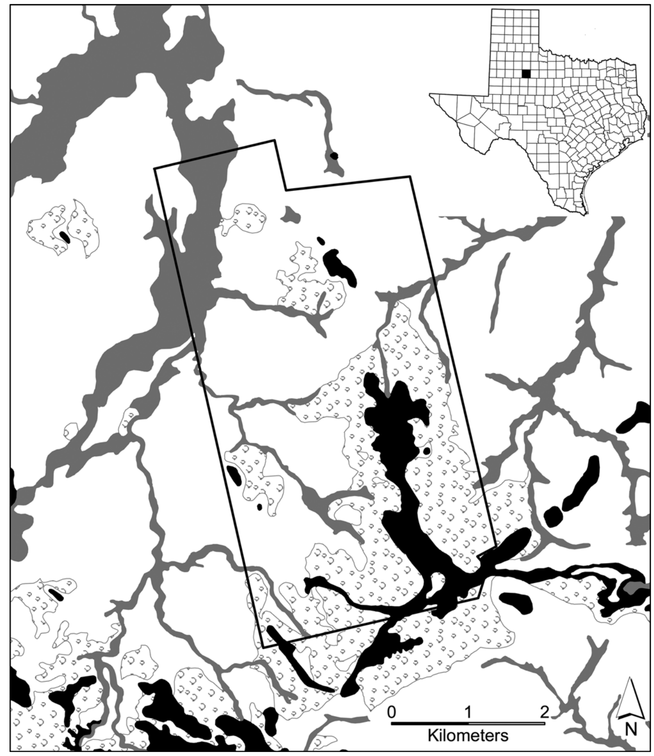

Figure 1. Distribution of major habitat types at the Rolling Plains Quail Research Ranch, Texas, USA, with inset showing study site location. Ranch boundary is outlined in black. White = grassland within the ranch, converted to cropland to the north and east and to mesquite-dominated rangeland to the south and west of the ranch; stippled = shrubby grassland; gray = riparian areas associated with the ephemeral creek system; black = rocky ridges.

trapped or hunted on the ranch for 3 years prior to and during this study.

METHODS

Animal Capture and Collaring Schedule

To track the nocturnal movements and habitat use by coyotes, raccoons, and bobcats, we fitted captured individuals with GPS collars (Lotek Wireless, Newmarket, ON, Canada) scheduled to collect data at 5-min intervals from 1830 hr to 0630 hr daily to cover the period when these nocturnal animals were most active. Average trial length was 33 nights/animal for bobcats and raccoons and 54 nights/animal for coyotes, which could carry a GPS collar with a larger battery pack. We applied differential correction to the collar data to reduce locational error to within 2.5 m (U.S. Coast Guard Navigation Center 2011).

Entry of animals into the project was staggered; capture of animals from which useable data sets were obtained were as follows. Throughout May and June of 2009 and 2010, we caught 4 female and 7 male raccoons in live traps (size 30 cm × 30 cm × 120 cm, made locally) placed throughout the ranch. We caught 3 male coyotes in May 2009 and 1 female coyote in May 2010 via aerial netting from a helicopter. We caught an additional male and a female coyote, in June 2010 and May 2011, respectively, in padded leg-hold traps (Oneida Victor #3 Softcatch, Euclid, OH). No bobcats were caught in the live or leg-hold traps, so in May 2011 we deployed large live traps (size 60 cm × 60 cm × 120 cm, made locally) containing a living rooster in a separate secure compartment and subsequently caught 1 female and 3 male bobcats. We sedated all animals caught in traps with Telazol (tiletamine HCl and zolazepam HCl; Pfizer, Inc., New York, NY). We used the manufacturer's recommendations for dogs and cats to sedate coyotes and bobcats, respectively; for raccoons we used a dosage of 4.3 mg/kg (*sensu* Gehrt 2001). Animal handling techniques were in accordance with Texas A&M Institutional Animal Care and Use Committee in Animal Use Protocol 2009–026 and Texas Parks and Wildlife Scientific Permit SPR 0405-067.

Spatial Distribution and Habitat Use

To assess the extent of area use by the animals we subsampled collar records at hourly time intervals to limit autocorrelation within our data (Swihart and Slade 1985*a*, *b*; Perotto-Baldivieso et al. 2012), before creating the 95% and 50% Kernel Home Ranges (KHR) with Home Range Extension for ArcView 3.2 (Carr and Rodgers 1998, Rodgers and Carr 1998). In this study, home range values pertain only to the summer distribution of each species; annual ranges may be larger. To obtain information on shared use of habitats, we assessed the degree of spatial overlap of area use within and between predator species by the proportional overlap of fixed-kernel home ranges (KHR) and core use areas. Overlap areas were not necessarily occupied simultaneously by the animals under investigation.

To assess habitat use, we developed a Geographic Information System layer of rangeland ecological sites from the Soil Survey Geographic database. Ecological sites are based on soil types but include information on topography that influences the distribution of vegetation. In turn, vegetation influences the distribution of food, cover, and possibly an obstruction to movement for animals (Dion et al. 2000). We calculated proportional occurrence of each ecological site at 2 second-order levels—within the ranch plus the surrounding 4-km buffer to encompass all areas used by the radiotagged animals (total area 18,688 ha), and just within boundary of the ranch in order to focus on the area in which known bobwhite nests were located. Based on the relatively fine spatial scale of interspersion of habitat types within the study area, we decided that it was appropriate to use the relatively similar temporal scale of 5 min to investigate selective habitat use by the animals (Reynolds and Laundrè 1990, Swain et al. 2008).

We used chi-squared tests (Manly et al. 2002) to compare percent available of each ecological site (expected data) with mean percent occurrence of GPS locations within each ecological site (observed data) for each species. In these tests, we incorporated uncommon ecological sites with <5% coverage with the most similar major ecological sites. We classified ecological sites as selected or avoided if proportional use by the animals was significantly ($P < 0.05$) higher or lower than availability. When assessing habitat use within the ranch, data from animals with <500 locations (<15% of data set) within the ranch boundary were excluded.

Nocturnal Paths of Mesopredators

We used Hawth's tools in ArcGIS 9.1 to calculate distance travelled by the animals each night. Reconstructing paths from locations taken at 5-min intervals misses fine-scale movements but does provide an estimate of minimum distance travelled. We assumed paths to be potential foraging and/or hunting paths, although locational data provide no specific information on the motivation determining animal movement. We applied fractal dimension to describe the degree of complexity of the animals' nocturnal paths. The program Fractal 5.0 (V.O. Nams, Nova Scotia Agricultural College, Truro, NS, Canada) uses the divider D, which is considered the best estimate for data from a continuous movement path (Nams 1996). Small differences in D indicate substantial changes in path tortuosity because of the exponential scaling relationship (Fuller and Harrison 2010). A fractal value of 1 depicts a straight line (e.g., when an animal is moving directly to a new location), and a value of 2 describes a tortuous path that completely covers a plane (as may occur when an animal is intensively searching an area; Bascompte and Vilà 1997). We obtained nocturnal paths for each animal on consecutive nights, and then averaged path length and tortuosity per animal and per species. We used 2-tailed t-test to detect differences in path statistics among species and between genders (Ruxton 2006).

Mesopredator Encounters With Quail Nest Sites

We drew information on known nesting locations of bobwhites from data collected in a separate study that used radiocollared bobwhite hens to determine breeding success of quail on the RPQRR (Rollins and Koennecke 2012). In this study we used data from 79 nests discovered during our study period from 2009 through 2011. Information was available on the location of each nest site and whether the eggs hatched or were lost to predation or abandonment of the nest.

The chance of a predator discovering a quail nest depends on the habitat selection, mobility and search pattern of the predator. To assess the relative risk posed by each predator species, we calculated the frequency with which nocturnal paths of the predators intersected with the 79 known current and former quail nest sites on the ranch. Distances over which bobcats, coyotes, and raccoons can detect quail nests are unknown; therefore, we buffered nest locations by 5 m, 10 m, 25 m, and 50 m, and then calculated how frequently nightly paths intersected each of these buffers. We expressed the frequency with which nightly paths of predators intersected nest-site locations as encounters per night. For comparison between species, we compared the frequency with which different predator species encountered nest sites with that of coyotes. Values are merely for comparison between species and calculated encounter rates should not be inferred to quantify actual rates of predation on quail nests. Whether or not there was an active nest with eggs at the moment a predator passed by a recorded nest site is unknown; furthermore, the predators likely had additional encounters with nests of non-radiomarked quail.

Table 1. Kernel Home Range (KHR) sizes (ha) of coyotes, bobcats, and raccoons during quail nesting season (May through Aug) at the Rolling Plains Quail Research Ranch, Fisher County, Texas, USA, 2009–2011.

		95% KHR		50% KHR core-use area	
Animal	***N***	**Mean**	**±SD**	**Mean**	**±SD**
Coyotes (M)	4	622	243	178	86
Coyotes (F)	2	402	220	75	45
Coyotes (all)	6	549	241	144	88
Bobcats (M)	3	1,286	263	336	141
Bobcats (F)	1	1,896		485	
Bobcats (all)	4	1,438	373	373	137
Raccoons (M)	7	727	330	201	95
Raccoons (F)	4	169	10	37	6
Raccoons (all)	11	512	369	148	84

RESULTS

Spatial Distribution of Mesopredators

During bobwhite nesting season, bobcats used large home ranges of 1,438 ± 373 ha (Table 1). There was minimal (<3%) overlap of 95% KHRs between male bobcats and no overlap of 50% core areas. Home range of the female was similar in extent to that of the males and had a 20% overlap of the core area of a single male. Although all bobcats were trapped within the ranch, each one ranged extensively beyond the ranch boundaries. One male and female bobcat spent 49% and 65% of their time on the ranch, respectively, but the other 2 bobcats spent most of their time (>95%) outside the ranch boundaries.

Home range sizes of coyotes were variable but were generally one-third the size of bobcat home ranges (95% KHR: $t_8 = 4.63$, $P = 0.002$). No gender difference was detected in the size of area used by coyotes (95% KHR: $t_4 = 1.07$, $P = 0.345$). Radiotagged coyotes were distributed within 4 distinct home ranges. Within the RPQRR, 2 male coyotes had completely overlapping 95% and 50% KHRs in the northern area; a male and female coyote shared a home range in the center of the ranch; and the female caught in 2011 inhabited the east side of the ranch. These 5 coyotes spent >95% of their time within the ranch boundaries, the 95% KHRs coyote family groups overlapped by 15% but there was no overlap of core use areas. The male coyote caught in the south of the ranch mainly lived south of the property (93%) and had no spatial overlap with the coyotes living on the ranch.

The 95% KHRs of male raccoons fell within extent of home ranges used by coyotes and bobcats. In contrast, female raccoons had small home ranges <20% the size of male ranges (95% KHRs: $t_9 = 3.30$, $P = 0.009$; 50% core areas: $t_9 = 3.37$, $P = 0.008$). Home ranges of raccoons showed extensive overlap within genders; within concurrent time periods some radiotagged males had completely overlapping 95% KHRs, while females displayed ≤66% overlap of home ranges. Within 50% core areas, spatial overlap was ≤91% for males and ≤27% for females. All raccoons ranged beyond the ranch boundaries and overall raccoons spent 55% ± 28% of their time on the ranch (range = 17–98%).

Nocturnal Habitat Selection of Mesopredators

Coyotes spent most of their time in open grassland (47% ± 26%) and mixed grass–shrub habitats (39% ± 22%). Within the entire area coyotes showed selective use of habitats (Table 2a). They avoided bare, fallow agricultural fields occurring mainly on loamy prairie soils and favored grass–shrub habitat on sandy loam sites. The 5 coyotes residing primarily within the ranch boundaries showed little selection for any particular ecological site within the ranch, other than slightly lower use of clay loam grassland (Table 2b).

Bobcats were selective of habitat within the entire area and spent the majority of their time (67% ± 15%) in habitats providing dense vegetation cover, particularly the riparian woodland associated with the creek system. When on the ranch, bobcats favored the riparian strip and grass–shrub habitat that provided good cover and they avoided open grasslands on clay loam and shallow soils.

Within the entire area, raccoons showed strong preference for riparian areas and rocky ridges. Raccoons were only recorded in open grassland for 8% ± 7% of locations and avoided fallow agricultural fields. Males, but not females, preferentially used the shrubby grasslands of the sandy loam ecological sites (male raccoons: $\chi^2{}_1 = 11.59$, $P < 0.001$). Within the ranch boundaries, raccoons were found predominantly in the riparian areas of Buffalo Creek or on the sides of the rocky ridge where there was ample cover. Raccoons of

Table 2a. Habitat use by mesopredators in the Rolling Plains Quail Research Ranch and surrounding 4-km buffer zone, Fisher County, Texas, USA, during May through August, 2009–2011.

		Animals					
	Ecological site	**Coyotes ($n = 6$)**		**Bobcats ($n = 4$)**		**Raccoons ($n = 11$)**	
Habitat	**% Availability**	**% Use**	χ^2	**% Use**	χ^2	**% Use**	χ^2
Clay loam grassland	15.54	10.47	1.65	12.48	0.60	5.44	$6.56^{\dagger\dagger}$
Loamy prairie grassland–crops	42.15	20.57	$11.05^{\dagger\dagger\dagger}$	32.91	2.03	17.73	$14.15^{\dagger\dagger\dagger}$
Shallow grassland	9.72	15.99	4.01	12.85	1.01	2.70	$5.07^{\dagger\dagger}$
Sandy loam grass–shrub	17.21	38.71	29.85^{***}	16.39	0.04	24.65	3.22
Loamy bottomland	10.50	8.00	0.59	21.17	10.86^{***}	31.32	41.30^{***}
Very shallow ridges	4.88	6.27	0.04	4.19	0.10	18.15	36.11^{***}
Sum $\chi^2{}_5$			44.58^{***}		14.63^{**}		106.41^{***}

Selected: $^{*}P \leq 0.050$, $^{**}P \leq 0.010$, $^{***}P \leq 0.010$; Avoided: $^{\dagger}P \leq 0.050$, $^{\dagger\dagger}P \leq 0.010$, $^{\dagger\dagger\dagger}P \leq 0.001$.

Table 2b. Habitat use by mesopredators and nesting bobwhites within the boundaries of Rolling Plains Quail Research Ranch, Fisher County, Texas, USA, during May through August, 2009–2011.

		Animals							
	Ecological site	Coyotes ($n = 6$)		Bobcats ($n = 4$)		Raccoons ($n = 11$)		Bobwhite nest sites ($n = 79$)	
Habitat	% Availability	% Use	χ^2	% Use	χ^2	% Use	χ^2	% Use	χ^2
Clay loam grassland	17.50	9.69	3.49†	5.11	8.78††	6.90	6.42††	18.99	0.13
Loamy prairie grassland	18.48	19.13	0.02	13.92	1.13	6.01	8.41††	26.58	3.55*
Shallow grassland	13.62	19.10	2.20	4.01	6.78††	3.04	8.21††	11.69	0.36
Sandy loam grass–shrub	30.83	37.88	1.61	45.18	6.68**	28.37	0.02	30.38	0.01
Loamy bottomland	10.78	8.79	0.37	22.51	12.75***	35.61	57.16***	11.39	0.03
Very shallow ridges	8.78	5.43	1.28	9.28	0.03	20.07	14.51***	1.27	6.43††
Sum χ^2_5			8.98		36.14***		58.84***		10.52

Selected: *$P \leq 0.050$, **$P \leq 0.010$, ***$P \leq 0.010$; Avoided: $^{\dagger}P \leq 0.050$, $^{\dagger\dagger}P \leq 0.010$, $^{\dagger\dagger\dagger}P \leq 0.001$.

both sexes used grass–shrub habitat in proportion to availability but avoided all types of open grasslands.

Nocturnal Movements of Mesopredators

At night coyotes travelled the longest paths (Table 3) of the 3 species of predators (bobcats $t_8 = 5.51$, $P < 0.001$; male raccoons $t_{11} = 4.24$, $P = 0.001$; female raccoons $t_7 = 6.91$, $P < 0.001$). Paths of coyotes were extensive and relatively linear (Fig. 2). Within a period of 1 month, the paths of individual coyotes covered virtually every part of their home range. Distances between final locations at dawn and first GPS readings at dusk indicated considerable diurnal activity by the coyotes. Nocturnal paths of bobcats were half the length of paths taken by coyotes, but were similar in distance to nightly paths of raccoons. Path tortuosity of bobcats was intermediate to that of coyotes and male raccoons. Male raccoons followed paths that were shorter and more tortuous than the paths of coyotes (Fractal values: $t_{11} = 5.39$, $P < 0.001$). Paths of female raccoons were often, but not consistently, shorter than those of males and more tortuous than those of all other predators (coyotes $t_{11} = 7.74$, $P < 0.001$; bobcats $t_6 = 5.06$, $P = 0.002$; male raccoons $t_9 = 5.83$, $P < 0.001$).

Encounter Rate of Mesopredators With Known Quail Nest Sites

Within the ranch boundaries, bobwhite nests were found in most habitat types (Table 2b). There was evidence of a weak preference for nesting in loamy prairie grasslands and against nesting on the rocky ridge. Nests located in areas classified as loamy bottomland were near grassy drainages and not within the densely treed riparian zone. Nests in grassland and in areas with greater vegetation cover were equally likely to be intersected within 50 m by the path of a coyote (grassland 84.4%, shrubland 84.9%). Nests in grassland were less often encountered by raccoons and bobcats (55.6% and 51.1%, respectively) than were nests in areas with greater vegetation cover (78.8% and 72.7%, respectively). Overall hatching success of nests was 43.0%. Hatching success varied by habitat ($\chi^2_4 = 22.05$, $P < 0.001$) and was greatest in grasslands associated with shallow ecological sites (66.7%); moderate in loamy prairie sites (52.4%), near drainage lines (44.4%), and in shrubby sandy loam areas (37.5%); and least in clay loam grasslands (26.7%).

Table 3. Lengths and fractal dimensions of nocturnal paths made by coyotes ($n = 6$), bobcats ($n = 4$), male raccoons ($n = 7$), and female raccoons ($n = 4$) from May to August, 2009–2011, at Rolling Plains Quail Research Ranch, Fisher County, Texas, USA.

		Path length (km/night)		Fractal dimension (D)	
Animal	Average paths/animal	Mean	±SD	Mean	±SD
Coyotes	53	8.99	1.46	1.08	0.01
Bobcats	32	4.60	0.71	1.10	0.01
Raccoons (M)	30	5.51	1.49	1.11	0.01
Raccoons (F)	33	3.49	0.71	1.18	0.03

Nightly encounter rates of individual mesopredators with known nest sites was low (Table 4). Over the entire area, and across all buffer widths, coyotes were approximately 3 times more likely to encounter a nest site than were male raccoons (within the 50-m buffer: $t_{11} = 2.29$, $P = 0.043$), and 7 times more likely to encounter a nest site than were bobcats ($t_8 = 2.37$, $P = 0.045$). None of the female raccoons came within 50 m of any of the 79 known nest sites. Coyotes spent proportionally more time within the ranch boundaries than did either of the other species, but even when examination is limited to only times when animals were present on the ranch coyotes were still 1.5 and 4 times more likely than male raccoons and bobcats, respectively, to encounter quail nest sites. On a weekly basis, within the boundaries of the RPQRR, individual coyotes came within 5 m of a known nest site (i.e., predation would be likely) approximately twice weekly (2.03 ± 1.26); male raccoons came within 5 m of a nest site once per week (1.19 ± 1.12), while bobcats came within 5 m of a nest site once every 3 weeks (0.35 ± 0.35).

DISCUSSION

We identified coyotes, and to a lesser extent male raccoons, as the mesopredator species with the greatest individual likelihood of encountering bobwhite nest sites. Rates of encounter with nest sites by bobcats and female raccoons were minimal.

We hypothesize that the greater encounter rate of coyotes with nest sites can be partially attributed to their selection for grassland and grass–shrub habitats (Litvaitis and Shaw 1980)

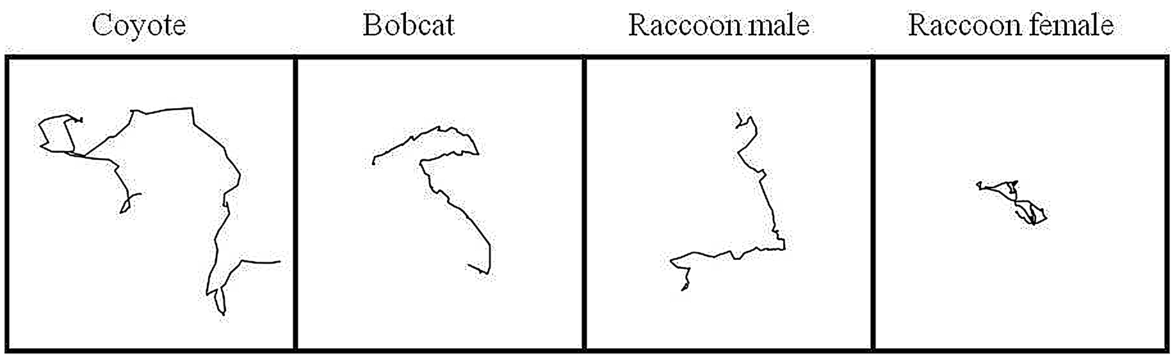

Figure 2. Representative nocturnal paths (1830–0630 hr) of mesopredators at the Rolling Plains Quail Research Ranch, Texas, USA, during April–August of 2009–2011. Selected paths are as close as possible to the mean fractal value (D) and length (m) for each species and gender and are drawn to the same scale. Actual values of displayed paths: Coyotes ($D = 1.085$, length = 8,964 m); Bobcats ($D = 1.095$, length = 4,541 m); Raccoon males ($D = 1.118$, length = 3,852 m); Raccoon females ($D = 1.180$, length = 3,857 m).

that are prime nesting habitat for bobwhites. The long nocturnal paths of coyotes (Andelt 1985, Servín et al. 2003) and extensive coverage of most areas within their home range, predisposes coyotes to encounter more bobwhite nests than would other, less cursorial, predators. The rapid movements and relatively straight paths of coyotes are predicted to be advantageous to animals searching for dispersed resources (Wiens et al. 1995), as is appropriate for coyotes hunting for vertebrate prey or detecting scattered quail nests.

The low encounter rates of bobcats and female raccoons with bobwhite nest sites was most likely a result of their strong preference for woodland and riparian habitats (Litvaitis and Harrison 1989, Tucker et al. 2007, Beasley and Rhodes 2010), which typically are not used as nesting habitat by bobwhites. On a nightly basis, bobcats (Elizalde-Arellano et al. 2012) and raccoons travelled only half as far as coyotes and their paths were more tortuous, possibly due to the physical constraints of movement within a spatially complex habitat (Fuller and Harrison 2010) and differences in foraging technique. Male raccoons were more likely than females to use areas with less dense cover (Beasley and Rhodes 2010) and consequently they had more frequent contact with bobwhite nest sites. Although primarily grassland birds, in this southern environment bobwhites require up to 30% shrub cover for thermal protection and predator escape cover (Hiller and Guthery 2005, Ransom et al. 2008), thus they often nest in shrub–grassland habitats. The slower, more tortuous nocturnal paths of raccoons were indicative of a more intensive search pattern than is shown by coyotes, although the area searched was less extensive. Theoretically, this more intensive searching should increase the chances of raccoons locating hidden resources such as quail nests (With 1994, Nams and Bourgeois 2004). Thus, coyotes and raccoons use 2 contrasting foraging strategies: coyotes display rapid searching of large areas, whereas raccoons have intensive searching of a smaller areas; however, both techniques are appropriate for discovering cryptic, scattered nests. Contact rate of raccoons with bobwhite nests in open grasslands was less than in shrubby areas, possibly because raccoons tend to change from a meandering path to more rapid and direct travel when crossing open habitats (Arditi and Dacorgna 1988, Newbury and Nelson 2007).

The behavioral ecology of the mesopredators reflected in the home range sizes in our study gives us some insight into

Table 4. Nightly encounter rate of mesopredators with 79 known bobwhite nesting sites, and ratio of encounters by coyotes in comparison with that of bobcats and raccoons at Rolling Plains Quail Research Ranch, Fisher County, Texas, USA, during 2009–2011. Total number of paths coyote ($n = 320$), bobcat ($n = 127$), raccoon male ($n = 210$), raccoon female ($n = 131$).

		Buffer size									
		5 m		10 m		25 m		50 m		Average ratio	
Animals	***N***	**Mean**	**±SD**	**Mean**	**±SD**	**Mean**	**±SD**	**Mean**	**±SD**	**Mean**	**±SD**
All areas											
Coyotes	6	0.27	0.18	0.58	0.36	1.35	0.77	2.61	1.76	1	
Bobcats	4	0.03	0.03	0.08	0.13	0.23	0.36	0.41	0.60	7.1	1.4
Raccoons (M)	7	0.08	0.07	0.20	0.15	0.51	0.39	0.92	0.80	2.9	0.4
Raccoons (F)	4	0		0		0		0		0	—
Only on the RPQRR											
Coyotes	6	0.29	0.18	0.62	0.38	1.42	0.79	2.74	1.49	1	
Bobcats	4	0.05	0.06	0.13	0.21	0.56	0.52	0.86	0.83	4.1	1.5
Raccoons (M)	7	0.17	0.16	0.44	0.40	1.03	0.81	1.74	1.33	1.5	0.2
Raccoons (F)	4	0		0		0		0		0	—

the risk that different mesopredators pose to nesting quail. The solitary nature of bobcats (Bailey 1974, Ferguson et al. 2009) and the large home-range sizes of individuals with little overlap within genders, suggests that the likelihood of bobcats encountering quail nests will be further limited by their low abundance in this prairie environment. Nest predation by bobcats is rarely considered to be a major threat to quail populations (Hernández et al. 1997, Tewes et al. 2002, Staller et al. 2005), although the extent and effects of their predation on chicks and adult birds is unknown. Coyotes are less solitary than bobcats and although home ranges usually have little to no overlap between adult animals of the same gender, pairs and subadults will share a home range (Windberg and Knowlton 1988, Schrecengost et al. 2009). This, along with the smaller size of coyote home ranges (Andelt 1985), allows the population density of coyotes to be higher than that of bobcats, consequently increasing the risk that coyotes may pose to nesting quail. A limited number of studies consider coyotes to be a major source of mortality for quail and their nests (Lehman 1984, Rader et al. 2007), but overall there is little evidence that nest predation by coyotes affects bobwhite populations (Henke 2002). In this study, the hatching success of bobwhite nests in grasslands inhabited mainly by coyotes was comparatively good, indicating that predation of nests by coyotes was not a major negative factor in the dynamics of the local bobwhite population. Raccoons differ from coyotes and bobcats in that they are much less territorial and show considerable spatial overlap between home ranges of individuals of the same gender (Gehrt and Fritzell 1998). Male raccoons, particularly in southern populations, tend to form stable coalitions often numbering 3–5 members (Walker and Sunquist 1997, Chamberlain and Leopold 2002, Gehrt et al. 2008). Overlap of same-sex home ranges can result in high population density and hence, due to their more social nature, raccoons may be a more serious predator of bobwhite nests than is indicated merely by the relative encounter rate of individual animals with nest sites. Raccoons, despite being individually less likely than coyotes to discover quail nests, are generally considered to be the most significant nest predator of quail in the Rolling Plains ecoregion (Rollins 2007), as well as in more shrub-dominated habitats to the south (Hernández et al. 1997, Cooper and Ginnett 2000, Staller et al. 2005).

The presence of multiple species of predators with different foraging strategies may increase risk of nest loss for bobwhites. Within habitats used by nesting bobwhites, overlap of core use areas of the 3 mesopredator species was small and occurred mainly in the grass–shrub habitat where there was additional cover for raccoons and bobcats. Although sample sizes are small, hatching success of bobwhite nests in this multi-use habitat was somewhat lower than for nests in more open grasslands on shallow soils used mainly by coyotes. Ranch management to reduce shrub cover in these areas may limit the activity of raccoons and improve nest survival, but then again, the observation that the lowest hatching rate occurred in clay loam grasslands that were not often used by any of these predator species, indicates the presence of other factors also affecting the bobwhite population.

Given the low encounter rate of individual predators with bobwhite nest sites, managers should consider the costs and benefits of predator removal programs before taking action (Jiménez and Conover 2001, Rader et al. 2011). In this prairie habitat, removal of bobcats will not improve the hatching success of bobwhite nests. Removal of coyotes has proved ineffective in boosting quail populations in the past (Henke and Bryant 1999) and could even be counter-productive if removal of this top predator allows incursion by smaller, but more abundant, nest predators into the grasslands (Crooks and Soulé 1999). Whether coyotes restrict the activities of raccoons is debated (Gehrt and Prange 2007), but coyotes can kill raccoons (Kamler and Gipson 2004, Tyson 2012) and the selection for cover and change in path dynamics of raccoons when crossing open grassland habitats may be indicative of avoidance of the larger predator.

One conundrum common in ranch management, and a confounding factor in this study (Jhala 2013), is the attraction of raccoons into quail nesting habitat by the provision of supplemental feed for game species (Cooper and Ginnett 2000, Henson et al. 2012). Another is that land management actions undertaken to promote better nesting success in quail and other grassland birds will also alter the habitat for the predators and may change the availability of the many alternative food sources used by these adaptable and omnivorous animals (Tyson 2012). Finally, although difficult to quantify, the relative effects of predation of juvenile and adult birds by the different mesopredator species should be considered (Rollins and Carroll 2001). Thus a more individualized and holistic approach may be required for predator management to enhance quail populations than merely the general removal of all potential nest predators.

MANAGEMENT IMPLICATIONS

Encounter rates of individual predators with quail nests were low, but if the decision is made to remove animals efforts should be focused on selective removal of the most abundant and problematic predators (e.g., raccoons) directly in the area where nests are being depredated. Alternative management options may include leaving some coyotes to possibly deter raccoons from foraging in prime nesting habitats, and/or selective manipulation of cover to limit the ability of raccoons to access bobwhite nesting areas.

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