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NORTHERN BOBWHITE HOME RANGE SIZES AND MOVEMENTS IN SOUTH TEXAS

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ABSTRACT

Northern bobwhites (Colinus virginianus) often have relatively small home ranges (<1-km radius); however, occasional long-distance movements also have been recorded, which may help maintain connectivity and genetic diversity within and among populations. We quantified movements of radio-collared northern bobwhites on the King Ranch in South Texas, USA. For each bird we determined core area, home range (fixed kernel), mean movement rate, and maximum distance moved. We compared movements across age, gender, precipitation trends, and plant communities using Mann–Whitney U and Kruskal–Wallis tests. Almost half (44.7%) of the birds moved >400 m (max. distance moved) and 46 (16%) moved >1 km over the course of the study. Males had higher movement rates (juvenile $\bar{x}=54.9$ m, SE = 1.77 m, n = 64; adult $\bar{x}=56.6$ m, SE = 1.95 m, n = 65) than females (juvenile $\bar{x}=51.26$ m, SE = 1.80 m, n = 102; adult $\bar{x}=48.14$ m, SE = 1.49 m, n = 62; $\chi^2_{3,289} = 14.90$, $P = 0.02$). Maximum distance moved was longer in dry years (609.8 ± 136.3 m) compared with normal or moist years ($\bar{x} = 542.8$ m, SE = 47.0 m; $\bar{x} = 536.6$ m, SE = 28.8 m, respectively, n = 293). Northern bobwhites moved farther in dry years, possibly to find cover and food. A small percentage made relatively long-distance movements (n = 18, 6%, >1.6 km, max. 6.5 km). These rare movements may influence gene flow and genetic structure of northern bobwhite populations in South Texas.


Key words: Colinus virginianus, habitat, Palmer Modified Drought Index, South Texas Quail Research Project, Texas Ecological Land Classification Project

Animal movements may be driven by competition for resources, competition for mates, and landscapes that lack necessary vegetation composition and/or patch sizes. Gene flow may improve genetic diversity if dispersers survive to reproduce in a new population. Conversely, reduced gene flow may result in lower genetic diversity if a species’ movement is limited (e.g., blue ducks (Hymenolaimus malacorhynchos; Triggs et al. 1992). Recurring fluctuations in populations with limited dispersal may act as small genetic bottlenecks. These populations may lose genetic diversity through genetic drift during phases of low population density (Nei et al. 1975). Bottlenecks and isolation can lead to large genetic variation among populations facing habitat fragmentation (e.g., eastern wild turkeys [Meleagris gallopavo silvestri]; Leberg 1991).

Most northern bobwhites (Colinus virginianus) have small home ranges (<30 ha; Yoho and Dinnick 1972, DeVos and Mueller 1993, Janke and Gates 2013) and are often found within 10 km of their original banding location (Stoddard 1931, Murphy and Baskett 1952, Smith et al. 1982, Lehmann 1984). Occasionally, northern bobwhites are capable of long-distance movements, sometimes travelling >100 km (Cooke 1946, Kiel 1976, Lehmann 1984:119). Research from the Caesar Kleberg Wildlife Research Institute indicates a weak genetic
structure ($\theta_{ST} = 0.037$, Wehland 2006; $F_{ST} = 0.015$, Miller 2014) for northern bobwhite populations in South Texas, USA. Gene flow, dispersal, or other factors may drive this weak genetic structure; thus, it is important to assess which factors compel northern bobwhites to move long distances.

Northern bobwhite reproduction and extreme population fluctuations are tied to rainfall (Bridges et al. 2001, Hernández and Peterson 2007, Rader et al. 2007, Tri et al. 2012) in South Texas. Herbaceous vegetation may be limited during years with below-average rainfall, forcing northern bobwhites to move farther in search of resources or potentially face local population declines (Peterson 2001). Thus, precipitation and temperature may affect availability of food and cover, movement, and gene flow of northern bobwhite populations.

Northern bobwhite behavior and abundance may also drive movement. In the autumn, northern bobwhite family groups may merge into one covey or break into separate coveys. This behavior is known as the covey shuffle (Lehmann 1984). Winter coveys may provide a source of mates in the spring. However, some birds must move farther in search of mates when coveys have uneven sex ratios and exhibit agonistic behavior (Lehmann 1984:50). Population density may also be a factor; Rosene (1969:80) recounted a mass movement of northern bobwhites on the Mississippi and Ohio riverbanks in the 1930s. These birds may have been attempting to move from populations of high density to those of lower density (Rosene 1969).

Whether rainfall or northern bobwhite behavior drives individual birds to disperse, there may be a gender or age bias to movement. Female-biased dispersal occurs in bird species, most likely because males defend the territories and females choose males based on territory quality. Among galliforms, female-biased dispersal has been documented in blue grouse (Dendragapus obscurus; Jamieson and Zwickel 1983), ruffed grouse (Bonasa umbellus; Small and Rusch 1989), and western capercaillie (Tetrao urogallus; Segelbacher et al. 2008). However, northern bobwhite dispersal appears slightly biased toward males (Stoddard 1931, Townsend et al. 2003). Age may be another potential bias; juveniles appear to disperse farther than adults (Smith et al. 1982, Townsend et al. 2003).

Previous research by the Caesar Kleberg Wildlife Research Institute provided an opportunity to study home ranges and movements of a northern bobwhite population in South Texas over a 7-year period (Rusk et al. 2006, Arredondo et al. 2007, DeMaso 2008). We compared core area, home range size, and movements of northern bobwhites across age and gender groups, varying annual and seasonal weather conditions, and land cover types that may influence home range and movement.

We tested 3 hypotheses to understand effects of age and gender, weather, and weather and plant community. Our first hypothesis was that juvenile males would have larger home ranges and longer movements, compared with females or adult males, than would be expected by chance. Our second hypothesis was that northern bobwhites would be more likely to disperse during dry years when food and cover may be limited. Our third hypothesis focused on weather and plant communities. We hypothesized that home ranges would encompass both grassland and mesquite-shrubland (Prosopis glandulosa) during years with normal precipitation as birds moved between feeding and loafing cover, compared with dry years when availability of grassland cover was more limited. In dry years we expected home ranges to be more frequently located in mesquite-shrubland.

**STUDY AREA**

Our study was conducted on the King Ranch, a private ranch in South Texas with mesquite shrubland throughout the property. The King Ranch covers 333,866 ha in portions of Brooks, Kleberg, and Kenedy counties with small portions in Jim Wells, Nueces, and Willacy counties. The ranch was managed for cattle grazing, oil and gas development, and hunting for large ungulates (e.g., white-tailed deer [Odocoileus virginianus]) and game birds, including northern bobwhite (Ashton and Snead 2010).

Biologists collected data for this study from the Encino division of the King Ranch in Brooks County. Biologists sampled 3 pastures as spatially independent units: North Viboras (1,966 ha), Loba (1,379 ha), and Cuates (1,240 ha). A north–south gradient of woody cover increased from Cuates (10% cover) and Loba (~25% cover) to North Viboras (>30% cover; Rusk et al. 2006). Dominant brush species that provided woody cover included honey mesquite, grangeño (Celtis pallida), huisache (Fachellia farnesiana farnesiana), live oak (Quercus virginiana), and prickly pear cactus (Opuntia engelmannii lindeimheri), Croton (Croton sp.), sunflower (Helianthus annuus), dayflower (Commelina erecta), and partridge pea (Chamaecrista fasciculata) were common forbs (Hernández et al. 2002). Grasses included little bluestem (Schizachyrium scoparium), paspalum (Paspalum sp.), threeawn (Artisida sp.), gulf cordgrass (Spartina spartinae), King Ranch bluestem (Bothriochloa ischaemum), sandbur (Cenchrus incertus), and buffelgrass (Cenchrus ciliaris; Hernández et al. 2002). The ranch had a semiarid climate with mean January temperature of 9ºC and mean July temperature of 35ºC. Mean annual rainfall was 56–66 cm with periods of drought (Rader et al. 2007). Droughts occurred approximately every 4–5 years during the course of the study.

**METHODS**

**Northern Bobwhite Movements**

Biologists trapped >2,000 northern bobwhites (DeMaso 2008) for the South Texas Quail Research Project from January through December of 1998–2008. They trapped birds using standard funnel traps (Stoddard 1931:442) and night-netting (Labisky 1968), fitted birds with an aluminum leg band, and then aged and sexed them (Rosene 1969). Biologists affixed a neck-loop transmitter (Shields et al. 1982; American Wildlife Enterprises, Tallahassee, FL, USA) to birds weighing
>150 g. Birds weighing <150 g (transmitter >5% of bird’s mass) were not radiomarked to limit potential effects of transmitters on northern bobwhite movement (Guthery and Lusk 2004). Handling procedures followed the protocols of the Texas A&M University-Kingsville Institutional Animal Care and Use Committee, permit 2003-3-3. Biologists determined locations of radiomarked northern bobwhites 3 times/week (DeMaso 2008) and all times of day to minimize diurnal peaks in activity. Triangulated locations were accurate to approximately 3 m (F. Hernández, Caesar Kleberg Wildlife Research Institute, Texas A&M - Kingsville, unpublished data). Biologists attempted to locate missing birds via fixed-wing aircraft after contact was lost with >5 birds (for cost-efficiency).

We used a subset from the data set (2000–2006) to determine northern bobwhite home range and movement. We eliminated locations where birds were found depredated because predators could have potentially moved the bird or the transmitter (Terhune et al. 2006). We then eliminated any bird with <20 locations (Haines et al. 2006, Brooke et al. 2015, Peters et al. 2015). We used the fixed-kernel method to determine core area and home ranges (Worton 1989) with a bandwidth of 100 m in ArcGIS (v. 10.1; ESRI, Inc. 2012, Redlands, CA, USA). The kernel density tool fits a curved surface over each point with a quadratic kernel function (Formula 4.5; Silverman 1986:76). Home ranges were defined as 100% kernels, and core areas were defined as the 50% density contour.

We determined linear movements for each bird, both mean movement rate and maximum distance moved. First we determined the distance between 2 consecutive locations and the number of days that elapsed between successive locations. We determined an index of mean movement rate, dividing the distance by the number of days and then averaging these values for each bird. Most (96%) successive locations occurred within 2 weeks. We removed all locations taken >1 week apart prior to determining mean weekly movement rates. We determined the maximum distance moved by each bird over the course of the study as the longest movement between 2 consecutive locations for that individual.

We measured the combined effect of rainfall and plant community type on northern bobwhite movements. For rainfall we used Palmer Modified Drought Indices and for plant communities we used the Texas Ecological Land Classification Project (Phase IV) developed by the Missouri Resource Assessment Partnership and Texas Parks and Wildlife Department. This map was developed using ecoregions, Soil Survey Geographic database, digital elevation model variables, hydrology, vegetation information, and ecological processes (fire, grazing, flooding, etc.), together with ground-truthing. Several plant communities occurred in the study area. Sandy mesquite savanna was characterized by grasses (little bluestem, coastal bermudagrass [Cynodon dactylon], Lehmman lovegrass [Eragrostis lehmanniana]). Deep sand grasslands were defined by gulf dune paspalum (Paspalum monostachyum), tanglehead (Heteropogon contortus), camphor weed (Heterotheca subaxillaris), partridge pea, and a smaller proportion of woody species (Baccharis [Baccharis spp.], prickly pear cactus, small honey mesquite). Salty prairie consisted of gulf cordgrass (Elliott 2011). We determined the plant community for each home range and core area if >50% of the area fell within the community type.

Statistical Analyses

All data failed tests for a normal distribution; therefore, we compared core areas, home ranges, mean movement rate, and maximum distance moved to northern bobwhite age, sex, weather, and plant community effects using Kruskal–Wallis tests. We conducted statistical tests with the R v. 3.3.1 statistical software (R Core Team 2016).

RESULTS

We estimated core areas, home ranges, and movements from 293 northern bobwhites. Mean core area was 3.40 ha (SE = 0.09 ha). Mean home range was 14.76 ha (SE = 0.36 ha). Mean movement rate was 52.54 m (SE = 0.87 m). Maximum distance moved was 666.23 m (SE = 36.91 m). Almost half (n = 131, 44.7%) of the northern bobwhites moved >400 m (one-quarter mile). Only 18 (6%) northern bobwhites moved >1.6 km. The longest distance moved between successive radiolocations (6.5 km) was by a second-year female banded near Cuates and found 52 days later at a nest with 12 eggs, in Loba.

Age, Gender, and Pasture Effects

Core area, home range, and maximum distance moved did not differ significantly across age and gender (Fig. 1). Adult females had lower movement rates (ß = 48.14, SE = 1.49, n = 62) than juvenile females (ß = 51.26, SE = 1.58, n = 102), juvenile males (ß = 54.95, SE = 1.77, n = 64), or adult males (ß = 56.36, SE = 1.95, n = 65; χ², 1, 289 = 14.90, P = 0.002; Fig. 1). Among the 18 birds that moved >1.6 km during the study (Fig. 2), movement rates did not differ among juvenile males,
juvenile females, or adult males ($\chi^2_{15} = 2.81, P = 0.246$). Only 3 of the 18 birds (17%) were adult females.

Mean movement rate differed across age, gender, and pasture ($\chi^2_{289} = 25.16, P = 0.009$; Fig. 3). Mean movement rate for juvenile females, adult females, and juvenile males decreased as woody cover increased from Cuates to North Viboras. Females in North Viboras had lower movement rates compared with birds

Fig. 1. Core area (ha), home range (ha), mean movement rate (m), and maximum distance moved (m) for northern bobwhites (Colinus virginianus) on the Encino Division of the King Ranch, South Texas, USA, during 2000–2006. Asterisk (*) denotes significant differences across age and gender, $\alpha = 0.05$. Error bars are standard error.

Fig. 2. Maximum distances (m) between consecutive radiolocations of northern bobwhites (Colinus virginianus) on the Encino Division of the King Ranch, South Texas, USA, during 2000–2006.
in other pastures and with males within North Viboras (Fig. 3).

Weather Effects

Mean home-range size was larger in normal years ($\bar{\chi} = 16.17$ ha, $\text{SE} = 0.58$ ha, $n = 124$) than in moist years ($\bar{\chi} = 12.68$ ha, $\text{SE} = 0.31$ ha, $n = 195$; $W 193 = 8,199$, $P < 0.001$; Fig. 4). Mean movement rates were similar in normal and moist years, but longer during dry years ($\chi^2_{2, 450} = 6.11$, $P = 0.047$). Northern bobwhites moved greater maximum distances in dry years ($\chi^2_{2, 450} = 7.35$, $P = 0.025$; Fig. 4).

Core area, home range, mean movement rate, and maximum distance moved differed across seasons and PMDI categories (Fig. 5). Home range was largest in normal summers ($\chi^2_{2, 308} = 39.47$, $P < 0.001$; Fig. 5). Movement rates were shortest in moist winters ($\chi^2_{2, 308} = 12.67$, $P = 0.005$). Maximum distance moved was also shortest in moist winters ($\chi^2_{2, 308} = 7.23$, $P = 0.027$; Fig. 5).

Weather and Plant Community Effects

Northern bobwhites occurred in all 3 plant communities defined by the Texas Vegetation Classification Project (Elliott 2011). Almost half ($n = 140, 48\%$) were in sandy mesquite savanna. Another 98 (33\%) were in deep sand grasslands. The remaining 56 home ranges (19\%) were located in salty prairie.

Home range and maximum distance moved differed among normal and moist years and plant communities. Home ranges were larger in normal years and smaller in moist years ($\chi^2_{5, 311} = 12.53$, $P = 0.028$; Fig. 6). Maximum distances moved were shorter in salty prairie in normal years ($\chi^2_{5, 439} = 15.28$, $P = 0.009$). No birds were found in deep sand grassland in dry years.

DISCUSSION

Northern Bobwhite Age, Gender, and Pasture Effects

We expected that northern bobwhite juvenile males would have larger home ranges and longer movement rates and maximum distances moved compared with females and adult males, based on previous observations (Stoddard 1931, Smith et al. 1982, Fies et al. 2002, Cook et al. 2006). Juveniles have been shown to have longer movements. For example, Fies et al. (2002) and Cook et al. (2006) found that juveniles were more likely than adults to make long-distance movements in the spring and summer. Males also tend to make longer movements (Stoddard 1931, Terhune et al. 2010, and Liberati and Gates 2012) as well as possess larger home ranges (Urban 1972, West et al. 2012). Therefore, the fact that adult males in our study had shorter movements but larger...
home ranges compared with juvenile males is interesting. It is possible that unpaired adult males in our study expanded home ranges as they searched for mates, similar to Urban (1972).

As expected, adult females in our study had the lowest mean movement rate. Adult females tend their nests and then make short movements with offspring. As offspring develop, females tend to make longer movements (Urban 1972, DeVos and Mueller 1993). Taylor et al. (2000) found that mean movement per day for incubating females averaged 357 m (SE = 54 m). However, mean movement per day increased to 503 m (SE = 60 m), once chicks fledged. Similarly, DeVos and Mueller (1993) found that northern bobwhite home ranges at Tall Timbers Research Station averaged 6.5 ha in the first 2 weeks posthatching and increased to 10 ha by the end of the first month.

Female northern bobwhites can and do move long distances. Fies et al. (2002) found that females moved farther (̅x = 1,328 m, SE = 187 m) than males (̅x = 1,068 m, SE = 100 m) in summer. Similarly, Cook et al. (2006) found that females made longer movements than males (F: ̅x = 2,173 m, SE = 319 m; M: ̅x = 1,576 m, SE = 230 m). The longest distance moved by a northern bobwhite in our study was by a second-year female (6.6 km). It is unclear whether she had a nest that failed prior to movement but that may be one impetus for female long-distance movement. Urban (1972) found that a hen in Illinois moved >2 km after her nest was destroyed.

Regardless of age, gender, or pasture, northern bobwhite movement rates were <65 m and mean maximum distances moved were <1 km (Fig. 3). Northern bobwhite movements are typically short (<8 km, Kiel 1976; <1.6 km, Lehmann 1984). It is possible that short daily movements in our study were due to the contiguous landscape that benefits northern bobwhite populations in South Texas.

Weather Effects

Weather has a significant effect on northern bobwhite populations in South Texas. Tri et al. (2012) found that variation in northern bobwhite age ratios could be attributed to rainfall (r² = 0.94). With adequate rainfall there should be sufficient food and nesting cover, which improves nest survival and should reduce the need for long-distance movements. In our study, northern bobwhites had larger home ranges in normal years compared with moist years and longer movement rates and maximum distances moved in drought years. This pattern held consistent over seasons (normal and moist summers, moist winters) as well.

Previous research on northern bobwhite movements and precipitation has found shifts in home range size (DeVos and Mueller 1993, West et al. 2012) and movements (Liberati and Gates 2012) with precipitation.
DeVos and Mueller (1993) determined that northern bobwhite at Tall Timbers Research Station had larger home ranges in the summer of 1985 (19.8 ha ± 2.18 SD) than in 1986 (12.3 ha, SD = 1.39; T = 2.91, P < 0.01). The beginning of summer 1985 was dry but a moist winter followed by a normal early summer in 1986 may have promoted vegetation growth. West et al. (2012) found that northern bobwhite home ranges in Kentucky were larger in 2009 (x̄ = 61.0 ha, SE = 10.4 ha) than in 2010 (x̄ = 44.9 ha, SE = 5.9 ha), which was a wetter year. Movements may also change with precipitation; summer movements for northern bobwhite in southwestern Ohio were significantly longer (4.13 ± 1.00 km) in one dry year (2010) compared with a wet year (2011, 2.66 ± 0.52 km; Liberati and Gates 2012).

In addition to precipitation, temperature has an important effect on northern bobwhites in South Texas (Tri et al. 2012). Northern bobwhite broods in Oklahoma moved greater distances when temperatures were lower, and moved shorter distances in midday and afternoon when temperatures were higher (Carroll et al. 2015). Tanner et al. (2016) found that usable space for northern bobwhites decreased when temperatures rose above 35°C.

Weather and Plant Community Effects

As expected, northern bobwhites occupied all 3 plant communities in normal years as birds moved from feeding to loafing cover. We expected that in dry years birds would use mesquite shrubland because northern bobwhites choose loafing cover with greater canopies on hotter days (Guthery et al. 2000). In dry years birds used saline prairie and sandy mesquite savanna but not deep sand grasslands. The mean movement rate was shorter in dry years and similar in normal and moist years.

Northern bobwhites use a variety of habitats in different stages of succession (Stoddard 1931, Rosene 1969, Lehmann 1984). Brooding, nesting, and roosting northern bobwhites selected sites with more cover in Kansas (Taylor et al. 1999). Pasture land with woody brush cover dominates the South Texas landscape. Woody brush cover has been shown to be a critical part of northern bobwhite habitat (Kopp et al. 1998, Janke and Gates 2013, DeMaso et al. 2014). Janke and Gates (2013) found that while woody cover accounted for 11–17% available habitat, it surrounded 49% of the covey locations in Ohio. Long-term simulations of northern bobwhite indicated that populations were 2–3 times larger.
in pastures with 11–32% woody cover compared with a pasture with 5% woody cover (DeMaso et al. 2014). The quality of woody cover available to northern bobwhites is important as well (Lee 1994, Fies et al. 2002) and may affect northern bobwhite home range and movements. Lee (1994) described studies in Louisiana pineland and Mississippi where northern bobwhites had large home ranges (58.4 ha and 282 ha, respectively). Lee (1994) attributed these large home ranges to a need to search farther for food and to habitat degradation. Additionally, Fies et al. (2002) found that birds moved longer distances in more fragmented habitats. Grassland and woody cover in Encino was more contiguous in the landscape and was managed as northern bobwhite habitat.

It is clear from this and previous studies that northern bobwhite individuals occasionally move long distances. At Encino, most movements were less than what might be expected from genetic information (Wehland 2006, Eo et al. 2010, Miller 2014, Williford et al. 2014). Short-distance movements as documented in this study may be adequate to facilitate gene flow to nearby ranches but do not explain the lack of genetic differentiation seen at a larger scale (for example, from South Texas to the Great Plains, $F_{ST} = 0.023$; Miller 2014). Given the longer movements made by some northern bobwhites, it is worth considering that some birds move far enough to reach nearby ranches and that a few birds might make long-distance movements, facilitating gene flow.

**MANAGEMENT IMPLICATIONS**

Northern bobwhite home ranges and movements were small (18 ha, 1 km), supporting previous assumptions that most northern bobwhites have small home ranges and short-distance movements. Northern bobwhites in this study chose plant communities that provided a variety of foraging areas, loafing cover, and nesting substrate. Providing a heterogeneous landscape of bare ground, herbaceous vegetation, and woody cover is important to management and conservation of northern bobwhite habitat.

Despite small home ranges and short movements, a small percentage (6%) of northern bobwhites made relatively long movements (>1.6 km). The potential gene flow resulting from such long-distance movements may be one of several factors driving the weak genetic structure of northern bobwhite populations in South Texas. Critical habitat is important to northern bobwhites that must adapt to changing conditions, while corridors that facilitate long-distance movements and dispersal are
important to maintain gene flow and sustain local populations because abundance varies with annual weather conditions. For these few long-distance movements made by northern bobwhites, it is critical that there is contiguous habitat or corridors to allow for movement among populations.

SUPPLEMENTARY INFORMATION

Reference S1. Literature cited in Tables S1 and S2, a literature review of northern bobwhite (Colinus virginianus) movements and home ranges. Table S1. Distance travelled for northern bobwhites (Colinus virginianus) in the United States, 1925–1975. Home ranges for coveys, rather than individuals, denoted with *.

Table S2. Home range summaries for northern bobwhite (Colinus virginianus) in the United States, 1925–1975. Home ranges for coveys, rather than individuals, denoted with *.

Table S3. Northern bobwhites (Colinus virginianus) that moved more than 1000 m between observations from 2000–2006 on the Encino Division, King Ranch, Texas. Core Area (50% kernel, ha) and home range (ha) over the course of the study are provided. Date refers to date of movement (maximum distance moved, m). Age: HY (hatch year; juvenile), SY (second year), TY (third year), and A (adult).

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