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Behavioral Responses at Distribution Extremes: How Artificial Surface Water Can Affect Quail Movement Patterns☆

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ABSTRACT

Supplementing wildlife populations with resources during times of limitation has been suggested for many species. The focus of our study was to determine responses of northern bobwhite (*Colinus virginianus;* Linnaeus) and scaled quail (*Callipepla squamata;* Vigors) to artificial surface-water sources in semiarid rangelands. From 2012–2014, we monitored quail populations via radio telemetry at Beaver River Wildlife Management Area, Beaver County, Oklahoma. We used cumulative distribution functions and resource utilization functions (RUFs) to determine behavioral responses of quail to water sources. We also used Program MARK to determine if water sources had any effect on quail vital rates. Our results indicated that both northern bobwhite and scaled quail exhibited behavioral responses to the presence of surface-water sources. Northern bobwhite selected for areas < 700 m and < 650 m from water sources during the breeding and nonbreeding season, respectively. However, the nonbreeding season response was weak ($\overline{\beta}$ = –0.06, SE = < 0.01), and the breeding season ($\overline{\beta}$ = 0.01, SE = 0.02) response was nonsignificant on the basis of RUFs. Scaled quail selected for areas < 650 m and < 250 m from water sources during the breeding and nonbreeding season, respectively. The breeding season RUF ($\overline{\beta}$ = –0.31, SE = 0.07) indicated a stronger response for scaled quail than bobwhite. Conversely, there was no direct effect of surface water on quail vital rates or nest success during the course of our study. Although water may affect behavioral patterns of quail, we found no evidence that it affects quail survival or nest success for these two species.

Introduction

Understanding the ecology of species at their distribution limits has important implications to conservation (Grinnell, 1917; MacArthur, 1972). Limits in a species' distribution can provide insight into examining potential constraints on populations, or how populations may adapt to unique conditions that infrequently occur within the core of a species' distribution (Sexton et al., 2009). The availability of resources for wildlife, such as food, water, and cover (Leopold, 1933), on distribution extremes may influence a species in ways that may not occur away from the periphery of its distribution. Furthermore, population responses and/or persistence can vary along gradients of resource and environmental variables, leading to the formation of distribution limits (Birch, 1953).

Sympatric populations of northern bobwhite (*Colinus virginianus;* hereafter "bobwhite") and scaled quail (*Callipepla squamata)* offer a unique opportunity to study the influence of limiting resources on space use and vital rates, as these populations typically occur on the western and eastern extremes of the species' distributions, respectively (Schemnitz, 1964). Within this region and other semiarid and arid rangelands, the importance of water as a potentially limiting resource has been emphasized and the supplementation of water to enhance wildlife habitat continues to be a subject of debate among biologists (Rosenstock et al., 1999). Recommendations for provision of artificial surface water may be a result of actual observable depletions of available surface water in ecosystems or from analogies of human situations in which water supplementation is necessary (Campbell, 1960).

Particular attention has been paid to providing surface-water sources to various species of quail in semiarid and arid rangelands (Glading, 1943), as the potential for population responses and economic payoffs is more likely in dry environments (Campbell, 1960). However, ambiguity in tangible benefits of surface water to quail has existed since early results from studies by Grinnell (1927) and Vorhies (1928),

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though many of these studies relied purely on observational data to support or refute any benefits of surface-water sources. Because of limited data and ambiguous results, researchers and managers continue to try to assess if and when quail respond and/or benefit from the presence of artificial surface-water sources.

Generally speaking, scaled quail tend to be more drought tolerant than bobwhite (Schemnitz, 1964) as they have better osmoregulation during times of extreme water deprivation (Giuliano et al., 1998). Because of this difference in physiology, a greater response of bobwhite to the provision of artificial surface-water sources in semiarid regions would be predicted. Although direct individual use of surface water has been documented in bobwhite populations (Lehman, 1984; Prasad and Guthery, 1986), results on population responses to artificial surface-water sources have been mixed. For instance, Guthery and Koerth (1992) determined that water supplementation did not benefit bobwhite, particularly when water was not a limiting factor. Conversely, Hiller et al. (2009) determined that both nonnesting bobwhite and bobwhite nest locations were located significantly closer to surface-water sources compared with random locations, whereas Dunkin et al. (2009) provided evidence of bobwhite breeding and nonbreeding selection to areas > 250 m and < 600 m from surface-water sources. Such studies suggest that bobwhite may be responding behaviorally to the presence of surface-water sources but do not indicate if such behavioral responses result in increased vital rates.

Similarly, there have been contrasting results when studying the response of scaled quail to surface-water sources. Direct use of surface-water sources have been documented for scaled quail, though at relatively low rates that may not be biologically meaningful (Campbell, 1960). Additionally, scaled quail in Oklahoma were observed at locations closer to water than would be expected at random, though it was not determined whether this behavior was from direct use of water or from responding to other elements of habitat such as vegetation (Schemnitz, 1961). Ultimately, it has been suggested that scaled quail may satisfy their water requirements from food sources and that providing surface-water sources is not necessary (Campbell et al., 1973).

In North America, an understanding of rangeland faunal responses to the provisioning of surface water will become increasingly important in future decades, as many of these rangelands are predicted to experience unprecedented droughts as a result of climate change (Cook et al., 2015). Furthermore, ground water withdrawal by humans often exceeds water recharge in aquifers within these rangeland systems (Dennehy et al., 2002; Moore et al., 2012), and recharge of these aquifers is predicted to be further reduced under future climate scenarios (Rosenberg et al., 1999). As such, the efficacy of providing artificial water sources for rangeland wildlife may be confounded by increased water demand and decreased water availability.

In this paper, we present results of the most comprehensive study to date examining bobwhite and scaled quail population responses to surface-water sources. By addressing multiple facets of potential population responses, we hope to provide greater insight as to whether surface water confers any benefit to these two quail species. We assessed the direct benefit of water provision through increased quail vital rates, changes in resource selection of quail from provision of surface water, and the confounding effects related to artificial surface water and vegetation cover. Our objectives were to determine if sympatric populations of bobwhite and scaled quail respond behaviorally to artificial surface-water sources in a semiarid region at the species' distribution extremes. More specifically, we wanted to determine at what spatial scale birds may be behaviorally responding to water, whether or not the probability of space use by quail increased as distance from water decreased, and quantify any differences in vegetation cover between used and unused water sources. We also sought to estimate any relation between quail vital rates (nest success and adult survival) and presence of surface-water sources that may ultimately influence overall population levels.

Methods

Study Area

Beaver River Wildlife Management Area (WMA), located in Beaver County, Oklahoma (lat 36°50'21.62"N, long 100°42'15.93"W), consists of approximately 11 315 ha managed by the Oklahoma Department of Wildlife Conservation (ODWC). Most of the WMA consists of upland rangelands and the floodplain of the Beaver River. Much of the upland areas are dominated by tivilo fine sand soils, whereas the floodplain is dominated by lesho silty clay loam. Dominant grasses on upland sites consist of buffalograss *(Buchloe dactyloides)*, little bluestem *(Schizachyrium scopariu)*, and bromes (*Bromus* spp.; non-native). Dominant forbs on upland sites include western ragweed *(Ambrosia psilostachya)*, queen's delight *(Stillingia sylvatica)*, and Texas croton *(Croton texensis)*. Dominant shrubs on upland sites include yucca *(Yucca glauca)*, sand sagebrush *(Artemisia filifolia)*, sand plum *(Prunus angustifolia)*, and fragrant sumac *(Rhus aromatica)*. Dominant grasses in the floodplain areas include weeping lovegrass (*Eragrostis curvala;* non-native), little bluestem, and switchgrass *(Panicum virgatum)*.

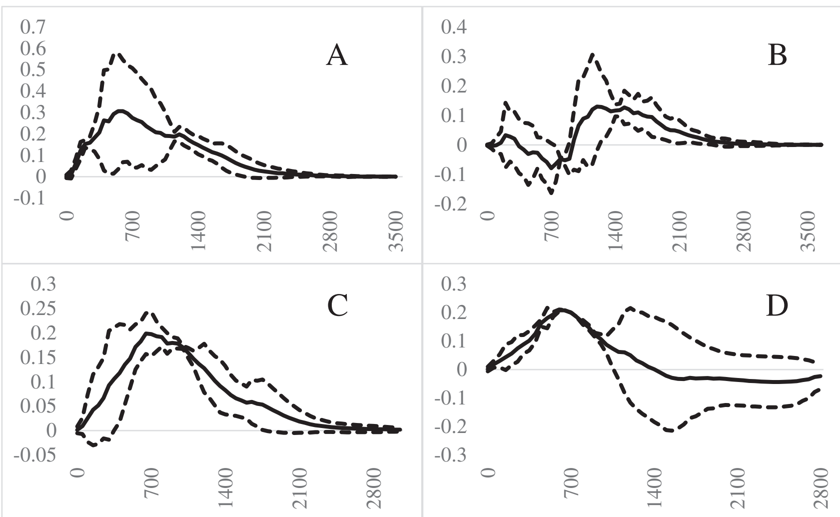

Fig. 1. Average selection-avoidance-neutral trends (solid lines) with 95% confidence limits (dashed lines) of scaled quail and northern bobwhite based on distance from artificial surface-water sources (m) from 1 April 2012–31 March 2014, Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA. **A,** Scaled quail breeding season. **B,** Scaled quail nonbreeding season. **C,** Northern bobwhite breeding season. **D,** Northern bobwhite nonbreeding season.

Table 1
Comparison of vegetation cover within northern bobwhite selection zones around used (breeding season $n = 34$; nonbreeding season $n = 24$) and unused (breeding season $n = 14$; nonbreeding season $n = 12$) artificial surface-water sources from 1 April 2012–31 March 2014 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA. Bold denotes significant differences ($\alpha = 0.05$)

Cover Class	Breeding season						Nonbreeding season					
	Used		Unused				Used		Unused			
	Mean	SE	Mean	SE	Z	P	Mean	SE	Mean	SE	Z	P
Riparian grassland	0.02	0.01	0.06	0.02	1.91	0.06	0.03	0.05	0.06	0.08	0.69	0.49
Bare ground	0.01	< 0.01	0.01	< 0.01	0.28	0.78	0.01	0.01	0.01	0.01	−0.82	0.41
Exposed soil/sparse vegetation	0.01	< 0.01	0.02	0.01	−0.42	0.67	0.01	0.02	0.01	0.01	−1.02	0.31
Mixed shrub	0.11	0.02	0.06	0.02	**−2.01**	**0.04**	0.11	0.09	0.08	0.12	−1.8	0.07
Salt cedar	0.02	0.01	0.03	0.01	0.86	0.39	0.03	0.04	0.02	0.04	0.16	0.87
Sand sagebrush	0.49	0.02	0.41	0.03	−1.62	0.10	0.50	0.15	0.40	0.09	**−2.03**	**0.04**
Mixed grass	0.18	0.01	0.23	0.02	1.76	0.08	0.18	0.08	0.24	0.09	1.86	0.06
Shortgrass/yucca	0.14	0.02	0.17	0.04	0.71	0.47	0.13	0.11	0.18	0.11	1.63	0.10

Dominant woody plants in the floodplain include fragrant sumac, sand plum, salt cedar (*Tamarix* spp.; non-native), eastern cottonwood *(Populus deltoides)*, and sugarberry *(Celtis laevigata)*. Western ragweed is the dominant forb in the floodplain areas.

Over the course of our study (2012–2014), average temperatures in summer ranged from 19.56–22.28, 25.72–27.22, and 26.78–30.06 °C during May, June, and July, respectively. The long term (1895–2014) average regional temperature during this period is 25.28 °C. Average temperatures in the winter ranged from −0.83 to 2.17, 1.28–1.33, and −0.33 to 2.39 °C during December, January, and February, respectively. The long-term average regional temperature during this period is −3.78 °C. Annual precipitation was 34.44, 50.29, and 39.42 cm in 2012, 2013, and 2014, respectively. The long-term annual precipitation for this region is 49.63 cm. Climate data were obtained from the Beaver Mesonet station (Brock et al., 1995; McPherson et al., 2007). During our data collection period (1 April 2012–31 March 2014), the WMA was classified under drought conditions ranging from severe to exceptional, and at no time was our study area out of drought conditions (The National Drought Mitigation Center, Lincoln, Nebraska). Management practices consist of cattle grazing (1 stocker · 16 acres, grazed for 150 days; only during 2012), strip discing, and food plot establishment.

Aerial imagery consisting of 2 × 2 m resolution was obtained during July 2012 and used in our classification of six major vegetation types across the WMA: sand sagebrush, shortgrass/yucca, mixed grass, mixed shrub, riparian grassland, and salt cedar. Anthropogenic surface-water sources (hereafter: water sources) consisted of windmills with water tanks, solar water wells, and gallinaceous guzzlers with overhead cover (Glading, 1943). There was only one permanent water source on our study site that was natural (pond < 0.01 ha), so we limited the scope of our analysis to artificial surface-water sources. Furthermore, we did not categorize water sources (i.e., guzzlers vs. windmills) in our analysis as the central focus of our study was to determine use of all anthropogenic water sources in general. Water sources were examined each season (breeding and nonbreeding) and year to confirm whether they provided water. From 2012–2013, the number of water sources functioning across the WMA decreased from 48 (2012) to 36 (2013). These 12 water sources were nonfunctioning because grazing on the WMA was discontinued due to continued drought conditions. As such, these water sources were not repaired after they ceased working. The density of water sources was 236 ha · water source in 2012 and 314 ha · water source in 2013 (Fig. S1; available online at http://dx.doi.org/10.1016/j.rama.2015.07.008).

Radiotelemetry

We captured bobwhite and scaled quail between February and October 2012–2013 using walk-in funnel traps (Stoddard, 1931). Captured quail were banded with leg bands (size 7) and fitted with a necklace-style radio transmitter weighing 6 g (crystal-controlled, two-stage design, pulsed by a CMOS multivibrator, Advanced Telemetry Systems, Inc., Isanti, Minnesota) based on meeting a minimum body mass requirement (130 g). As our study area was located along the Beaver River corridor, areas used by scaled quail within the boundaries of the WMA were restricted primarily to the upland boundaries that were shared with private landowners. This limited the trapping efforts, and ultimately our sample size, for scaled quail during our study in comparison with bobwhite, which were located throughout the majority of the WMA.

Radio-marked individuals were located a minimum of three times per week using a scanning receiver and a handheld Yagi antenna (Advanced Telemetry Systems, Inc.). We located quail by homing (White and Garrot, 1990) within 15 m and recorded the distance and azimuth to the actual quail location while also marking the Universal Transverse Mercator coordinates of the observer with a global positioning system (GPS) unit (Garmin International, Inc., Olathe, Kansas). We recorded locations of quail at different times on subsequent days to capture the variability of diurnal patterns. To accomplish this, we grouped birds by different sections of the WMA and alternated the order in which each section was monitored across days. Our trapping and handling methods

Table 2
Comparison of vegetation cover within scaled quail selection zones around used (breeding season $n = 13$; nonbreeding season $n = 7$) and unused (breeding season $n = 35$; nonbreeding season $n = 29$) artificial surface-water sources from 1 April 2012–31 March 2014 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA. Bold denotes significant differences ($\alpha = 0.05$)

Cover Class	Breeding season						Nonbreeding season					
	Used		Unused				Used		Unused			
	Mean	SE	Mean	SE	Z	P	Mean	SE	Mean	SE	Z	P
Riparian grassland	0.01	0.01	0.04	0.01	**−2.39**	**0.02**	0.02	0.02	0.03	0.01	−1.00	0.32
Bare ground	0.01	< 0.01	0.01	< 0.01	−0.97	0.33	0.01	< 0.01	0.02	< 0.01	−0.20	0.84
Exposed soil/sparse vegetation	0.02	0.01	0.01	< 0.01	0.63	0.53	0.01	< 0.01	0.03	0.01	−0.64	0.52
Mixed shrub	0.08	0.03	0.10	0.02	−1.00	0.32	0.12	0.05	0.09	0.02	0.84	0.40
Salt cedar	< 0.01	< 0.01	0.03	0.01	**−2.63**	**< 0.01**	< 0.01	< 0.01	0.02	0.01	−0.91	0.36
Sand sagebrush	0.53	0.04	0.44	0.02	**2.00**	**< 0.05**	0.54	0.06	0.40	0.03	1.88	0.06
Mixed grass	0.22	0.03	0.19	0.01	0.91	0.37	0.18	0.04	0.21	0.02	−0.68	0.50
Shortgrass/yucca	0.13	0.03	0.16	0.02	−0.95	0.34	0.11	0.05	0.19	0.03	−1.48	0.14

Table 3
Total cover and use of preferred vegetation types[1] by scaled quail and northern bobwhite during the breeding season (1 April–30 September) from 2012–2013 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA

		Scaled quail				Northern bobwhite			
		2012		2013		2012		2013	
Vegetation type	Total cover (%)	Use	CI	Use	CI	Use	CI	Use	CI
Sand sagebrush	36	0.43	0.38 to 0.48	0.42	0.38 to 0.45	0.54	0.52 to 0.57	0.52	0.49 to 0.54
Mixed shrub	8	–[2]	–[2]	–[2]	–[2]	0.29	0.27 to 0.32	0.28	0.26 to 0.31
Salt cedar	2	–[2]	–[2]	–[2]	–[2]	–[2]	–[2]	0.03	0.02 to 0.04
Mixed grass	18	0.25	0.21 to 0.29	0.22	0.19 to 0.25	–[2]	–[2]	–[2]	–[2]

[1] Selection determined by analysis described by Neu et al. (1974).
[2] Dashes indicate the vegetation type was not preferred during a particular year or for a particular species.

comply with the protocol determined by Oklahoma State University's Institutional Animal Care and Use Committee Permit (no. AG-11-22).

Cumulative Distribution Functions

Cumulative distribution functions (CDFs) were used to determine selection-avoidance-neutral behavior of quail in relation to distance from water sources during the breeding and nonbreeding seasons. We defined the breeding season as 1 April–30 September and the nonbreeding season as 1 October–31 March (Burger et al., 1995*a*). A form of this method of analysis was presented by Kopp et al. (1998) and subsequently used by Dunkin et al. (2009) in a similar analysis of anthropogenic structure effects on bobwhite. This analysis provides a continuous method of determining selection-avoidance-neutral behavior for data with large sample sizes and allowed us to determine the spatial scale at which quail were responding to water sources. Such large sample sizes can often lead to statistical significance in a model without any biologic meaning (Abelson, 1995; Guthery, 2008). CDFs are also beneficial in that we are able to use the entirety of our location data in the analysis. Dunkin et al. (2009) describes deriving an estimate of selection-avoidance-neutral behavior by subtracting the relative cumulative frequency ($G[x]$) of used locations by the cumulative frequency ($F[x]$) of random locations ($G[x] - F[x]$). CDFs are the integral of probability density functions (Wackerly et al., 2002) and thus can be useful in determining selection-avoidance behavior in relation to continuous resource variables (Dunkin et al., 2009). This equation creates a function in which a positive slope in the function indicates selection, a negative slope indicates avoidance, and a slope nearing 0 indicates a neutral relationship. The $G(x) - F(x)$ function was calculated for every 50-m interval (i.e., 0–49.99 m, 50–99.99 m, etc.), and we pooled these estimates between years for both breeding and nonbreeding seasons for both bobwhite and scaled quail. We determined a nonsignificant relationship if confidence limits overlapped 0, which would result from increased variability between years.

Thirty random points (Martin et al., 2012) were created for every water source within our study area. We then estimated the Euclidean distance (m) from bird locations to artificial surface-water sources and random (or "pseudo" water source) locations. A total of 30 iterations were carried out in which pseudo-water sources were randomly selected from our pool to estimate a bird's location to a pseudo-water source. The number of pseudo-water sources randomly selected for each iteration was equivalent to the number of actual water sources present across the WMA at the specific time period.

To account for the potential confounding effects of vegetation on selection of areas close to artificial surface-water sources, we determined any differences in vegetation cover within selection buffers around used versus nonused water sources using PROC NPAR1WAY in SAS 9.4 (Statistical Analysis System Institute Inc, Cary, North Carolina). The selection buffer was based on a radius equal to the maximum distance (m) from a water source in which selection behavior was determined. We assumed a water source was used if a bird location was within selection buffers around individual water sources. A utilization-availability analysis, as outlined by Neu et al. (1974), was used to determine vegetation types that were selected more than expected by bobwhite and scaled quail. We used the results from our utilization-availability analysis to compare % cover of selected vegetation types within and outside selection zones, while also relating this to the proportion of total bird points within and outside selection zones. Thus if the majority of a representative vegetation type was outside the zone of selection but the majority of points were within the zone of selection, we concluded that vegetation was not the sole driver of quail space use.

Space Use and Resource Utilization Functions

To validate relationships estimated from the CDFs, we also estimated the relationship of distance to surface-water sources on estimated probability of space use by a bird by estimating resource utilization functions (RUF; Marzluff et al., 2004; Millspaugh et al., 2006). RUFs allowed us to directly compare space use to distance from surface-water sources for individual birds during the breeding season and for coveys during the nonbreeding season. Space use by individual quail within coveys is nonindependent (Brooke et al., 2015; Janke and Gates, 2013); therefore we estimated RUFs for coveys during the nonbreeding season to meet the assumption of independence of space use between individuals (Marzluff et al., 2004). The RUF method is more advantageous than other resource selection methods because it treats each individual as the experimental unit rather than each location and restricts the space use of a bird to an estimated home range rather than by an arbitrary

Table 4
Total cover and use of preferred vegetation types[1] by scaled quail and northern bobwhite during the non-breeding season (1 October–31 March) from 2012–2014 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA

		Scaled quail				Northern bobwhite			
		2012–2013		2013–2014		2012–2013		2013–2014	
Vegetation type	Total cover (%)	Use	CI	Use	CI	Use	CI	Use	CI
Sand sagebrush	36	0.47	0.43–0.52	0.45	0.41–0.48	0.47	0.45–0.50	0.52	0.50–0.54
Mixed shrub	8	–[2]	–[2]	–[2]	–[2]	0.36	0.33–0.38	0.31	0.29–0.33
Salt cedar	2	–[2]	–[2]	–[2]	–[2]	0.03	0.02–0.04	–[2]	–[2]

[1] Selection determined by analysis described by Neu et al. (1974).
[2] Dashes indicate the vegetation type was not preferred during a particular year or for a particular species.

Table 5
Total hectares and proportion of preferred vegetation type (cover[1]) compared with proportion of the total study area and proportion of northern bobwhite locations within and outside the zone of selection surrounding artificial surface-water sources from 1 April 2012–31 March 2014 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA

	Breeding season				Nonbreeding season			
	Available cover (ha)	% Cover	Total area (%)	Locations (%)	Available cover (ha)	% Cover	Total area (%)	Locations (%)
Within selection buffer	3 372	48	49	62	2 335	33	34	56
Outside selection buffer	3 643	52	51	38	4 680	67	66	44
Total	7 015	100	100	100	7 015	100	100	100

[1] Cover is the total percent cover of selected vegetation types, which were determined by methods described by Neu et al. (1974). Selected vegetation types by northern bobwhite during the breeding and nonbreeding seasons were sand sagebrush, mixed shrub, and salt cedar.

boundary (Marzluff et al., 2004). As CDFs use the entire population of bird locations to assess the influence of a resource variable on space use, RUFs allowed us to confirm the estimated relationship on the basis of a subsample (individual birds or coveys with > 20 locations) of our location data. For instance, if a CDF indicated an attraction to surface water, the RUF would allow us to determine if the concentration of locations became denser as the distance from water lessened.

Seasonal home ranges for individuals or coveys having ≥ 20 radiotelemetry locations (DeVos and Mueller, 1993; Taylor et al., 1999) were created using the 95% fixed-kernel method (Seaman et al., 1999; Worton, 1989) through the Geospatial Modelling Environment (Spatial Ecology LLC, Marshfield, Wisconsin). A 95% limit was used to better compare our results with previously published literature that estimates quail space use (Janke and Gates, 2013; Lohr et al., 2011; Peters et al., 2015). The likelihood cross-validation bandwidth estimator was used to obtain kernel density (KDEs) estimates (Horne and Garton, 2006), which provided us with a unique smoothing parameter (*h*; Worton, 1989) for each individual that we subsequently used in our RUF calculations.

Utilization distribution rasters were created for each bird by assigning a use value ranging from 1–95% based on the relative volume of the utilization distribution (Kerston and Marzluff, 2010; Marzluff et al., 2004). The utilization distributions were constrained to each bird or covey's 95% volume contour determined from the previous step. Each cell was 10 × 10 m, which was also representative of the resolution of our distance-to–surface water environmental layer. Once utilization distributions were created, we extracted use and distance to water (m) values to points centered within every cell located in the utilization distribution. The distance-to–surface water layer was estimated using the Spatial Analyst Euclidian Distance tool in ArcGIS 10.2 (ESRI, 2011).

After extracting use and distance to water values within each home range, the relationship of space use to distance from water was estimated on a cell-by-cell basis, which produced a coefficient of resource use for each individual. We used the Ruf.fit package in Program R (ver. 3.1.1, R Foundation for Statistical Computing, Vienna, Austria) to estimate coefficients of resource use for our sample. To stay consistent with methods from our CDF analysis, we only computed RUFs for individuals that had the entirety of the estimated home range within the boundary of Beaver River WMA. Estimates of space use were $\log_e$-transformed to meet the linearity assumption for multiple regression models. To estimate the influence of surface water on our overall population, mean standardized β coefficients ($\overline{\beta}$) were calculated by season and species with conservative estimates of variance that incorporates interindividual variation (Marzluff et al., 2004). We considered standardized coefficients to be statistically significant if 95% confidence intervals did not overlap 0. Furthermore, a *t* test was used to test the significance of our standardized coefficients against a null model where of $\overline{\beta} = 0$ ($\alpha = 0.95$; Marzluff et al., 2004). Because our resource variable was a distance (m) measure, negative coefficients indicated that surface water had a greater than expected effect on space use, while positive coefficients indicated that surface water had a less than expected effect on space use (Marzluff et al., 2004). Finally, the number of individual birds or coveys that had significant positive, negative, or nonsignificant relationships to surface water were determined to display differences among individuals (Winder et al., 2013).

Survival Analysis

To determine if the presence of surface-water sources had any influence on bobwhite and scaled quail survival, we estimated seasonal survival rates coded on weekly time intervals (26 total intervals) using the known fate model with a logit link function in Program MARK for each species and season combination (White and Burnham, 1999). We censored the first 7 days after a bird was released in our analysis to control for potential short-term effects of capturing and radio-marking (Guthery and Lusk, 2004) and used a staggered-entry method to analyze survival with the known fate model (Pollock et al., 1989). This method left-censors individuals' encounter histories until they are captured and enter the monitored population. We right-censored individuals because of emigration from the study area, radio failure or loss, or when unknown fates occurred. We only analyzed survival of birds that had ≥ 20 locations and had estimated home ranges that were completely within the boundary of our study site so that we could maintain consistency with our other analyses.

We included group metrics (age, sex, season, and home range size [ha]) and variables related to surface-water sources determined by our previous analyses (presence of water in a home range, number of an individual's locations within our zone of selection, and RUF β coefficients) in our survival analysis to address our research objective. We also included a temporal and null model in our analysis. For the nonbreeding season, RUF β coefficients were estimated for individuals on the basis of covey associations. We used a ΔAIC_c value of < 2 (Burnham and Anderson, 2002) to determine the most parsimonious model for explaining variance in survival. However, we assumed that any exploratory variables contained in models performing worse than our null model did not contribute any relative importance to quail survival.

Table 6
Total hectares and proportion of preferred vegetation type (cover[1]) compared with proportion of the total study area and proportion of scaled quail locations[2] within and outside the zone of selection surrounding artificial surface-water sources from 1 April 2012–31 March 2014 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA

	Breeding season				Nonbreeding season			
	Available cover (ha)	% Cover	Total area (%)	Locations (%)	Available cover (ha)	Percent Cover (%)	Total area (%)	Locations (%)
Within selection buffer	3 272	47	44	65	296	6	6	9
Outside selection buffer	3 713	53	56	35	4 750	94	94	91
Total	6 985	100	100	100	5 046	100	100	100

[1] Percent cover is the total percent cover of vegetation types being selected for which were determined by methods described by Neu et al. (1974). Selected vegetation types by scaled quail during the breeding season were sand sagebrush and mixed grass and sand sagebrush during the nonbreeding season.

Table 7
Mean standardized resource utilization function coefficients ($\overline{\beta}$)[1] and percentage of birds with positive (+), negative (–), or nonsignificant (ns) β values[2] indicating the relationship of space use to distance from artificial surface-water sources (m). Data are provided for northern bobwhite and scaled quail during breeding and nonbreeding seasons 1 April 2012–31 March 2014 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA

Sample set	n	$\overline{\beta}$	95% CI[1]	+	-	ns	P value[3]
Bobwhite breeding season	80	0.01	−0.04 to 0.06	39	51	10	0.63
Bobwhite nonbreeding season	25	-0.06	−0.064 to −0.063	16	44	40	< 0.001
Scaled quail breeding season	10	-0.31	−0.44 to −0.17	0	80	20	< 0.01

[1] Confidence intervals were estimated based on conservative standard errors that include interanimal variation (Marzluff et al., 2004).
[2] The resource variable being tested is a distance-based variable. As such, a negative β value indicates an increase in space use as an individual gets closer to an artificial water source.
[3] The P value indicates a test against a null hypothesis of $\overline{\beta} = 0$ as described by Marzluff et al. (2004; $\alpha = 0.05$).

Nesting

Beyond adult survival, we also tested whether artificial surface-water sources had any influence on nest success. Quail were considered to be nesting if they were located at identical subsequent locations in the breeding season (Burger et al., 1995*b*). Once a bird was nesting, we marked (by GPS) the location near the nest while the radio-marked quail was present. We located the actual nest when the radio-marked quail was away from the nest or after hatch or abandonment. Once a quail was nesting, the incubation status (whether the quail is still nesting) was monitored daily by locating the radio-collared adult. We continued to monitor nests until they hatched or failed. A nest was defined as successful if ≥ 1 egg hatched. We compared the Euclidean distance (m) of successful and unsuccessful nests to surface-water sources and to pseudo water sources (random points). Randomization of pseudo-water source locations was identical to the methods described for our CDF analysis. Statistical significance of successful and unsuccessful nest distances to water and pseudo water sources was estimated on the basis of the nature of the 95% confidence intervals (Hiller et al., 2009).

Estimates of nest location distances to surface-water sources were pooled between species because of a low sample size for scaled quail nests ($n = 12$). Variance between successful and failed nests was unequal (F-value $= 2.94$; $p < 0.01$), therefore the Satterthwaite confidence limits were used to test for significance using PROC TTEST in SAS 9.4.

Results

During the study, radio transmitters were placed on 487 bobwhite and 131 scaled quail. From this sample, we obtained a total of 5 569 and 6 180 bobwhite breeding season and nonbreeding season locations, respectively, and 1 108 and 1 922 scaled quail breeding season and nonbreeding season locations, respectively. We were able to estimate home ranges for 80 bobwhite and 10 scaled quail in the breeding season and 25 bobwhite and 2 scaled quail covey ranges during the nonbreeding season. During the 2012 and 2013 breeding season, we located a total of 61 nests, of which 49 were bobwhite and 12 were scaled quail.

Table 8
Ranking of a priori models based on ΔAIC_c values used to assess the influence of group metrics and surface water source variables on northern bobwhite survival from 1 April 2012–31 March 2014 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA

Model	AIC_c	Δ AIC_c	AIC_c weights	Model likelihood	No. parameters	Deviance
Null	17.8	0.0	0.19	1.00	1	15.8
Water in home range	18.1	0.3	0.16	0.85	2	14.1
Home range size (ha)	18.2	0.4	0.16	0.84	2	14.2
Sex	18.6	0.8	0.13	0.70	2	14.5
Season	18.8	1.0	0.12	0.61	2	14.8
Age	19.1	1.3	0.10	0.53	2	15.1
RUF β	19.8	2.0	0.07	0.38	2	15.8
No. locations by water	19.8	2.0	0.07	0.37	2	15.8
Time	64.7	46.9	0.00	0.00	26	11.3

Table 9
Ranking of a priori models based on ΔAIC_c values used to assess the influence of group metrics and surface water source variables on scaled quail survival from 1 April 2012–31 March 2014 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA

Model	AIC_c	ΔAIC_c	AIC_c weight	Model likelihood	No. parameters	Deviance
Home range size (ha)	29.8	0.0	0.67	1.00	2	25.3
Season	33.9	4.1	0.07	0.13	2	29.4
Null	34.0	4.2	0.08	0.12	1	31.9
No. locations by water	34.2	4.4	0.07	0.11	2	29.8
Sex	35.7	5.9	0.03	0.05	2	31.2
Water in home range	35.9	6.1	0.03	0.05	2	31.4
Age	36.3	6.5	0.03	0.04	2	31.8
Time	73.0	43.2	0.00	0.00	26	13.9

Cumulative Distribution Functions

On the basis of slopes of our CDFs, both bobwhite and scaled quail locations were closer to artificial surface-water sources than expected (Fig. 1). Scaled quail exhibited significant selection for distances 100–650 m in the breeding season (Fig. 1A). Scaled quail exhibited a much weaker response to surface-water sources during the nonbreeding season compared with the breeding season. Specifically, a positive relationship was indicated from 50–250 m; however, this was not significant on the basis of confidence intervals and the overall sample resulted in a weak sigmoidal relationship (Fig. 1B). Bobwhite exhibited significant selection behavior at distances of 350–700 m from water sources during the breeding season, whereas they selected for distances of 50–650 m during the nonbreeding season (Fig. 1C and D).

For bobwhite, there were a total of 34 and 24 surface-water sources that were considered used during the breeding and nonbreeding seasons, respectively (Table 1). During the breeding season, water sources considered used by bobwhite had more mixed shrub cover within the zone of selection compared with water sources considered unused. During the nonbreeding season, water sources considered used by bobwhite had more cover of sand sagebrush within the zone of selection compared with water sources considered unused. Not surprisingly, because of sample size and habitat requirements, scaled quail used fewer water sources than bobwhite, with only 13 and 7 used during the breeding season and nonbreeding season, respectively (Table 2). During the breeding season, water sources considered used by scaled quail had less cover of salt cedar and riparian grassland and more cover of sand sagebrush within the zone of selection when compared with water sources considered unused. Water sources considered used by scaled quail during the nonbreeding season had no significant differences in vegetation cover within the zone of selection when compared with water sources considered unused.

Our utilization distribution analysis resulted in four vegetation types being used more than expected (Tables 3 and 4). From these results, we determined the proportion of these selected vegetation types within their respective zones of selection around all water sources for each species and each season, as well as the proportion outside of the zones of selection (Tables 5 and 6). For both species, there were more locations within zones of selection than would be expected on the basis of the proportion of selected vegetation types also within zones of selection, excluding the nonbreeding season scaled quail sample. Specifically, during the breeding season, scaled quail exhibited the most pronounced

Table 10
Distance (m) of pooled northern bobwhite and scaled quail nests to artificial surface-water sources and random locations from 1 April 2012–31 March 2014 at Beaver River Wildlife Management Area, Beaver County, Oklahoma, USA

Sample	n	Distance to water sources (m)		Distance to random locations (m)		P value[1]
		x	SE	x	SE	
Nests						
Successful	31	755.0	66.0	969.3	52.9	**0.01**
Failed	30	821.8	112.7	1 002.3	69.9	0.18
Total	61	787.9	64.4	985.6	43.3	**0.01**

[1] Bold P values denote significant differences between distances from nests to water sources compared with distance from nests to random locations ($\alpha = 0.05$).

relationship, in which 65% of their locations were within the zone of selection with water (<650 m) while 53% of the total available preferred vegetation types were located outside the zone of selection (see Table 6). Likewise, bobwhite during the nonbreeding season exhibited a strong relationship, in which 56% of their locations were within the zone of selection with water (<650 m) and 67% of the total available preferred vegetation types were located outside this zone (see Table 5).

Resource Utilization Functions

After filtering our sample of individuals to the boundary of the WMA, we were able to estimate RUFs for 117 individuals. A total of 10 RUFs were estimated for scaled quail individuals in the breeding seasons and two coveys in the nonbreeding seasons. We estimated 80 RUFs for bobwhite individuals in the breeding seasons and 25 coveys during the nonbreeding seasons. As our sample of estimable RUFs for scaled quail coveys was low ($n = 2$), we did not attempt to obtain $\overline{\beta}$ for this sample.

Results from our RUF analysis concurred with the CDF relationships we estimated for our scaled quail breeding season and bobwhite nonbreeding season samples (Table 7). Though our sample for breeding season scaled quail individuals was relatively low compared with our bobwhite sample, the $\overline{\beta}$ coefficient indicated a strong positive influence of space use related to distance from artificial surface-water sources ($\overline{\beta} = -0.31$, SE = 0.07, 95% CI = –0.44 to –0.17). Likewise, space use by nonbreeding bobwhite was positively related to distance from artificial surface-water sources ($\overline{\beta} = -0.06$, SE = 0.0002, 95% CI = ––0.064 to –0.063), although this effect was much weaker than the scaled quail relationship. Space use related to distance from artificial surface-water sources for bobwhites during the breeding season was not significant ($\overline{\beta} = 0.01$, SE = 0.02, 95% CI = –0.03–0.06).

Adult and Nest Survival in Relation to Water

A total of 146 bobwhite and 28 scaled quail individuals were used in our survival analysis. For our bobwhite sample, no models performed better than the null model, suggesting we did not include variables that strongly influenced bobwhite survival (Table 8). Home range size (ha) was considered the best performing covariate in explaining scaled quail survival ($\beta = -0.014$, SE = –0.026 to –0.002) and no water variables performed above the null model (Table 9). We were unable to include the RUF β coefficient as a variable in our scaled quail survival analysis because of our low sample size. However, the β model for our bobwhite sample was not considered to be a competing model as it performed worse than our null model.

The mean difference of distance from surface water between successful and failed nests was –66.8 m (SE = 128.9, 95% CI = –327.7 to 196.0), indicating there was no statistical difference between these samples as confidence intervals overlapped 0 (Table 10). However, successful nests (and the pooled sample of all nests) were closer to artificial water sources compared with pseudo-water sources ($P = 0.01$), whereas failed nests were not significantly closer to actual water sources when compared with their distance to random locations ($P = 0.18$).

Discussion

We found that northern bobwhite and scaled quail exhibited a behavioral response to the presence of artificial surface-water sources in a semiarid rangeland. These results were most pronounced for scaled quail during the breeding season. Bobwhite behavioral responses were weaker, particularly within 350 m of water. These results indicated that placement of artificial surface-water sources in a semiarid rangeland can influence quail behavioral patterns, at least in some years. Furthermore, we found that quail were selecting areas closer to water even when appropriate vegetation cover was available away from surface-water sources. This relationship indicates that there was a direct influence of surface water to the behavioral responses observed during our study beyond that which was driven by coarse scale vegetation cover and composition alone.

Our nesting results indicate that nest-site selection may be influenced by the presence of artificial surface-water sources. However, nest success was unaffected by the presence of these water sources. Previously, bobwhite have been shown to locate nests closer than expected to surface-water sources, though no difference in the distances between hatched and failed nests to water was observed (Hiller et al., 2009). Inhibition to reproduce and reproductive failure can occur when quail are exposed to water deprivation (Cain and Lien, 1985; Giuliano et al., 1995; Guthery and Koerth, 1992), so there may be benefits in locating nests closer to surface-water sources during times of potential stress from water loss. However, drought occurred during the entirety of our study and yet there was no relationship between nest success and distance from water sources. Therefore nesting quail were likely obtaining water from other sources such as food or dew (Guthery, 1999). To our knowledge, there is no study relating nest site selection to the presence of surface-water sources for scaled quail. Unfortunately, the low sample size ($n = 12$) during our study did not allow us to compare interspecific differences in behavioral responses of bobwhite and scaled quail when choosing a nest site.

The weak bobwhite behavioral response occurring closer to water sources was similar to results from other semiarid regions of the bobwhite's distribution in which nonsignificant use occurred at distances < 250 m (Dunkin et al., 2009). Although the $\overline{\beta}$ for breeding bobwhite did not indicate a significant effect toward surface-water sources, more than 50% of the birds in the sample had β estimates indicating a significant positive relationship with space use and distance to surface water. As discussed earlier, needs for water supplementation of bobwhite are typically not supported (Guthery, 1999), though this may be influenced by preformed water sources already available in the environment (Hernández et al., 2007). Furthermore, bobwhite behavioral responses to surface-water sources may be related to bobwhite seeking thermal refugia at water sites (via guzzlers) or to increased food availability from better soil moisture conditions (Hiller et al., 2009). Although we do not rule out these possibilities, our results also indicate nonbreeding season behavioral responses, in times when these alternative benefits (particularly thermal refugia) may not be occurring.

Similar to bobwhite, scaled quail also exhibited behavioral responses to surface-water sources during the course of our study, though a nonsignificant relationship was observed at close distances (<100 m) during the breeding season. Little research exists exploring such responses of scaled quail to surface water, and those that do exist provide mixed conclusions (Campbell, 1960; Schemnitz, 1961). The physiological differences between scaled quail and bobwhite in relation to water requirements (Giuliano et al., 1998) could allow for the prediction that scaled quail responses to surface water should be weaker compared with bobwhite. Furthermore, because our study site is on the distribution limits of both species, adaptive behavioral responses to novel climate conditions could be expected (Sexton et al., 2009) in which bobwhite may have stronger responses to surface water, though this was not supported by our breeding season data. Typical precipitation levels present within these species' respective distributions vary drastically (Giuliano et al., 1999; Robinson, 1956; Schemnitz, 1964), and scaled quail are considered to be more adapted to arid environments than bobwhite (Schemnitz, 1964). However, response to and use of surface-water sources by desert Galliformes have been widely documented (Delehanty et al., 2004; Kam et al., 1987; Larsen et al., 2007; Lynn et al., 2008; O'Brien et al., 2006).

We observed ambiguous relationships between site selection and areas within distances adjacent to water sources (i.e., 0–350 m), which resulted in neutral selection. A few factors could have contributed to these ambiguous results. Dunkin et al. (2009) indicates that mutually contradicting effects between a structure and the area it is located in may result in a neutral relationship closer to the structure. For instance, if a water source was indeed acting as an attractant but was situated in a cover type that is avoided by quail, the net result may be a neutral relationship. Furthermore, this neutral relationship may be a result of a potential trade-off between resource use (and time allocated for using that resource) and predation risk (Brown, 1999). However, we were not able to directly test this hypothesis with our data.

Water sources (such as guzzlers) could potentially increase quail survival by providing needed cover during critical weather events. Conversely, indirect negative effects, such as predation, could be more pronounced at artificial surface-water sources if water was limited during times of drought by potentially creating predator sinks (Hall et al., 2013; Rosenstock et al., 1999). However, data generally suggest that predation of varying wildlife species is not more pronounced at watering sites in semiarid and arid regions (Hall et al., 2013; Krausman et al., 2006). Our results suggest there are no direct effects of surface water to quail survival.

The density of available water sources on our study site was 236 ha · water source in 2012 and 314 ha · water source in 2013. Previous recommendations have suggested a density of 121 ha · water source (Hernández and Guthery, 2012). On the basis of our CDFs, the presence of artificial surface-water sources affected quail movement up to ~ 700 m for bobwhite and ~ 650 m for scaled quail. Taking the maximum value of the two, an ideal distribution (from a quail behavioral standpoint) of artificial surface-water sources across our study site would result in ~ 1400 m between each surface water source. This would result in a density of 1 water source per 154 ha, which may already exist on many rangelands in which grazing of livestock occurs within the distribution of bobwhite and scaled quail.

Implications

We found that artificial surface-water sources affected quail behavior but not vital rates. We suggest that management efforts focused on increasing or sustaining quail populations through water supplementation on semiarid rangelands are unfounded. Because bobwhite and scaled quail can often obtain sufficient water through arthropods and succulent vegetation (Campbell et al., 1973; Guthery, 1999), managing conditions that increase vegetation cover and arthropod abundance may be more effective in conserving quail populations than providing artificial surface-water sources.

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