Received: 23 March 2021 | Revised: 12 January 2022 | Accepted: 21 January 2022

DOI: 10.1002/jwmg.22209

RESEARCH ARTICLE

THE JOURNAL OF WILDLIFE MANAGEMENT

THE WILDLIFE SOCIETY

Quail and rain in semiarid rangelands: Does management matter?

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Funding information

Reversing the Quail Decline Initiative (Texas AgriLife); Texas Parks and Wildlife Department; South Texas Chapter of the Texas Quail Coalition, and East Foundation

Abstract

Rainfall is a strong driver of quail populations on southwestern rangelands and can account for a large portion (~70–95%) of the variability in regional quail production and abundance. Landowners have attempted to moderate these boom-and-bust fluctuations via management; however, presently it is unknown whether management can increase or stabilize quail populations in semiarid environments or whether rainfall remains as influential at small spatial extents. Our objectives were to evaluate the efficacy of management at mitigating the effects of rainfall on northern bobwhite (*Colinus virginianus*) populations on semiarid rangelands and to quantify the influence of rainfall on bobwhite density at smaller spatial extents. We conducted a study to evaluate these objectives during 2014–2020 in the Rio Grande Plains ($n = 11$ sites; 1,100–6,500 ha) and Rolling Plains ($n = 4$ sites; 1,900–4,000 ha) of Texas, USA. We estimated bobwhite density during late autumn (Dec–Jan) on all sites using helicopter surveys within a distance-sampling framework. We also obtained site-level seasonal rainfall (Apr–Aug) and quantified management intensity via landowner surveys and a scoring rubric to categorize sites into 3 classes (low, medium, and high management intensity). Bobwhite populations during this study experienced a boom-bust cycle in both the Rio Grande Plains and Rolling Plains, with mean bobwhite

[†]Deceased

density fluctuating considerably (0.57–2.96 bobwhites/ha and 0.02–2.88 bobwhites/ha, respectively). In the Rio Grande Plains, mean bobwhite density significantly increased from low to high management intensity in 2015 (1.12 ± 0.17 bobwhites/ha vs. 2.87 ± 0.39 bobwhites/ha, respectively), 2016 (1.06 ± 0.20 bobwhites/ha vs. 2.96 ± 0.36 bobwhites/ha, respectively), 2017 (0.73 ± 0.16 bobwhites/ha vs. 1.91 ± 0.32 bobwhites/ha, respectively), and 2019 (0.42 ± 0.14 bobwhites/ha vs. 1.01 ± 0.26 bobwhites/ha, respectively; $P < 0.05$). In addition, rainfall at the site level accounted for a low amount of the variation in bobwhite density ($r^2 = 0.09$; $P < 0.01$). Similarly, in the Rolling Plains, mean bobwhite density significantly increased from low to high management intensity in 2015 (1.30 ± 0.27 bobwhites/ha vs. 2.20 ± 0.29 bobwhites/ha, respectively) and 2016 (1.26 ± 0.26 bobwhites/ha vs. 2.88 ± 0.34 bobwhites/ha, respectively; $P < 0.05$). Rainfall at the site level also accounted for a low amount of the variation in bobwhite density ($r^2 < 0.02$; $P = 0.82$). Our findings suggest that management can increase bobwhite density beyond that of less-managed properties but does not completely eliminate inter-annual fluctuations in semiarid environments. In addition, rainfall appears to exert less of an influence on bobwhite density at a site level (e.g., 2,000 ha) than has been documented at a regional level (e.g., ≥8 million ha).

KEYWORDS

drought, hierarchy theory, northern bobwhite, quail density, rain, scale, wildlife management

The influence of rain on southwestern quail populations is well documented (Swank and Gallizioli 1954, Campbell et al. 1973, Kiel 1976, Brown 1989). Rain, or the lack thereof, is known to affect many aspects of quail life history including calling behavior (Gonzalez-Sanders et al. 2017), breeding success (Campbell 1968), nest initiation (Wallmo 1954), productivity (Tri et al. 2012), and survival (Hernández et al. 2005, Tri et al. 2016). The influence of rain is so strong that it can account for a large portion (~70–95%) of the variability in regional quail abundance (Bridges et al. 2001) and productivity (Tri et al. 2012). Consequently, quail populations inhabiting semiarid rangelands often fluctuate so considerably—increasing during periods of abundant rain but decreasing during drought—that their population dynamics have been described as a boom-and-bust phenomenon (Lehmann 1953).

Quail managers have attempted to stabilize the boom-and-bust dynamics of quail populations via intensive management (Brennan 2007, Hernández and Guthery 2012). Management strategies have included habitat-based approaches and cultural practices. Habitat-based approaches have included grazing management (Campbell-Kissock et al. 1984, Smith 2017), brush management (Guthery and Rollins 1997, Cooper et al. 2009), prescribed fire (Wilson and Crawford 1979, Carter et al. 2002), and discing (Webb and Guthery 1982, Hernández et al. 2009). Cultural practices have involved provision of supplemental feed (DeMaso et al. 2002, Guthery et al. 2004, Buckley et al. 2015), supplemental water (Guthery and Koerth 1992), and predator management (Guthery and Beasom 1977, Ellis-Felege et al. 2012). Given the economic importance of quail on these rangeland systems (Connor 2007), most quail-management programs consist of a suite of practices that are implemented across thousands of hectares in an attempt to maintain huntable quail populations in the face of variable rain (Howard 2007). Quail management on southwestern rangelands therefore tends to be intensive and extensive.

Despite the large amount of resources and time invested in quail management, the use and effectiveness of quail management is uncertain, especially in semiarid environments. If rainfall accounts for a large portion of the variability in regional quail abundance and production (Bridges et al. 2001, Tri et al. 2012), then theoretically only a small portion of this variance is left for management to influence. Such profound influence of rainfall may suggest that quail management in semiarid rangelands is a futile endeavor. However, the influence of rainfall on quail populations may vary by scale, with rainfall possibly exerting a greater influence on quail populations at large spatial extents (e.g., ≥4 million ha) but a lesser influence at smaller spatial extents (e.g., 2,000 ha; Hernández 2020). If rainfall is less influential at smaller scales, then other variables such as those that can be influenced by management (e.g., brush cover, grass height) may assume greater importance (Hernández 2020).

The degree to which management influences quail populations in semiarid rangelands remains unknown. In addition, whether rainfall exerts a lesser influence on quail abundance at smaller spatial extents, the scale at which management occurs, has not been evaluated. We evaluated the efficacy of management for increasing northern bobwhite (*Colinus virginianus*; bobwhite) density and modulating population fluctuations in semiarid environments and to quantify the influence of rainfall on bobwhite density at small spatial extents. We hypothesized that bobwhite density would increase (and temporal variability would decrease) with increasing management intensity and rainfall would account for a lower proportion of the variability in bobwhite abundance at smaller spatial extents (site level) than has been documented at larger spatial extents (ecoregion level). We use the term quail throughout this manuscript when generally referring to quails and the term bobwhite when specifically referring to northern bobwhite.

STUDY AREA

We conducted this study in the Rio Grande Plains (n = 11 sites) and Rolling Plains (n = 4 sites) ecoregions of Texas, USA (Gould 1975) because they support significant bobwhite populations and provide relatively large amounts of habitat (Hernández et al. 2007, Rollins 2007). Bobwhite populations in these 2 ecoregions are strongly influenced by rainfall and therefore are characterized by boom-and-bust population fluctuations (Figure 1; Hernández et al. 2007, Rollins 2007).

Rio Grande Plains

We collected data on 11 sites in the Rio Grande Plains ecoregion (Table 1). The Rio Grande Plains is an ecoregion with flat to undulating topography and with elevations ≤305 m (Gould 1975, Landers 1987). The climate for this ecoregion is semiarid and is characterized by periods of extreme fluctuations in temperature and precipitation. Mean annual precipitation is 500–750 mm, with peak rainfall occurring in May–June and September (Norwine and John 2007). Temperatures range from mean monthly minimum of 6.1°C (Jan) to mean monthly maximum of 36.2°C (Jul; 1895–2019; National Climatic Data Center 2021). Vegetation communities in the Rio Grande Plains include dense shrublands, grasslands, and savannas (Gould 1975, Landers 1987). Many species of woody plants are prevalent and have spread throughout this ecoregion including honey mesquite (*Prosopis glandulosa*), blackbrush (*Vachellia rigidula*), guajillo (*Senegalia berlandieri*), catclaw (*Senegalia greggii*), and spiny hackberry (*Celtis ehrenbergiana*; McMahan and Inglis 1974, Scifres 1980, Landers 1987). Soils in this ecoregion range from clays to sands (Correll and Johnson 1979). Common soil series include the Delmita series (fine-loamy, mixed, active, hyperthermic Petrocalcic Paleustalfs), Nueces series (mixed, active, hyperthermic Arenic Paleustalfs), and Sarita series (loamy, mixed, active, hyperthermic

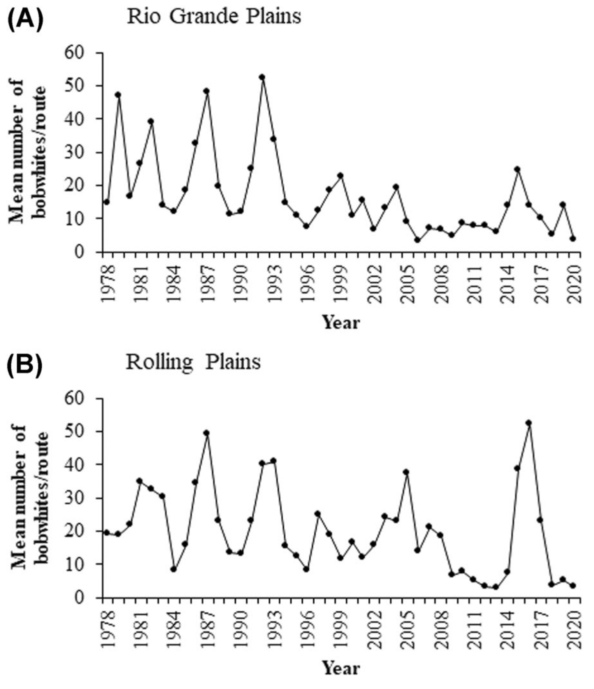

FIGURE 1 Relative abundance of northern bobwhite in the Rio Grande Plains (A) and Rolling Plains (B) of Texas, USA, 1978–2020. Data were provided by Texas Parks and Wildlife Department and collected using roadside surveys

Grossarenic Paleustalfs; U.S. Department of Agriculture 2021). Sandy soils are dominated by grasses including seacoast bluestem (*Schizachyrium littorale*), bristlegrasses (*Setaria* spp.), and paspalums (*Paspalum* spp.; Landers 1987). Clayey sites tend to have grasses such as longspike silver bluestem (*Bothriochloa longipaniculata*), buffalograss (*Bouteloua dactyloides*), and common curly mesquite (*Hilaria belangeri*; Landers 1987). Dominant fauna include white-tailed deer (*Odocoileus virginianus*), javelina (*Tayassu tajacu*), coyotes (*Canis latrans*), and wild turkey (*Meleagris gallopavo*).

Study sites in the Rio Grande Plains were separated by 20–70 km and spanned 2 counties (Duval, Jim Hogg; Smith 2017, Bruno 2018, Edwards 2019, Ritzell 2020). The sites collectively encompassed 30,043 ha. Habitat-management practices varied by site and included cattle grazing, chemical and mechanical brush management, prescribed fire, and discing. Cultural practices also varied by site and included supplemental feeding, supplemental water, and predator management. Sites ranged in management objectives from being mostly working ranches (livestock focus) to recreational ranches (bobwhite focus). Thus, sites exhibited variability in intensity of quail management that included different combinations and intensities of land-management and cultural practices.

Rolling Plains

We collected data on 4 sites in the Rolling Plains ecoregion (Table 1). The Rolling Plains ecoregion is characterized by slightly rolling topography, occasional steep slopes, large agricultural operations, and rangelands (Gould 1975, Landers 1987). Mean annual precipitation ranges from 558 mm to 762 mm and most frequently occurs during May and September (Correll and Johnson 1979, Landers 1987). Temperatures range from mean monthly minimum of −2.0°C (Jan) to mean monthly maximum of 35.4°C (Jul; 1895–2019; National Climatic Data Center 2021).

TABLE 1 General description of study sites used in research evaluating the influence of management intensity and rainfall on northern bobwhite density, Rio Grande Plains and Rolling Plains, Texas, USA, 2014–2020. We calculated percent rangeland within a 7-km buffer of study site's centroid point

Ecoregion Site	County	Area (ha)	Survey month	Number of transects	Annual survey effort (km)	Years	Rubric	Landowner self-score	Bobwhite density (bobwhites/ha) $\bar{x}$	Bobwhite density (bobwhites/ha) SE	Rainfall (Apr–Aug; mm) $\bar{x}$	Rainfall (Apr–Aug; mm) SE	% Rangeland
Rio Grande Plains													
1	Jim Hogg	1,529	Dec	19	64–77	2014–2019	Low	1 (Low)	0.57	0.09	24.7	3.2	99.90
2	Jim Hogg	1,518	Dec	23	56–76	2014–2019	Low	1 (Low)	0.84	0.15	24.7	2.1	99.99
3	Jim Hogg	6,588	Dec	19	161–180	2014–2019	Low	2 (Low)	1.22	0.25	26.0	3.0	99.69
4	Jim Hogg	1,264	Dec	19	60	2014–2019	Low	1 (Low)	0.64	0.18	23.4	2.8	99.94
5	Jim Hogg	1,248	Dec	9	35	2015–2019	Medium	5 (Medium)	1.65	0.26	22.4	3.0	99.21
6	Jim Hogg	3,641	Dec	18	67–99	2015–2019	Medium	5 (Medium)	1.83	0.56	28.1	4.0	99.10
7	Jim Hogg, Duval	5,012	Dec	26	128–203	2014–2016, 2019	Medium	7 (Medium)	1.41	0.38	32.9	6.6	99.47
8	Jim Hogg	2,737	Dec	15	76	2014–2019	Medium	7 (Medium)	1.37	0.31	24.1	2.1	99.72
9	Jim Hogg	1,133	Dec	11	30	2015–2019	Medium	5 (Medium)	1.26	0.37	21.0	2.9	99.57
10	Jim Hogg	1,552	Dec	15	42	2015–2019	High	10 (High)	2.24	0.39	21.2	2.7	99.44
11	Jim Hogg, Duval	3,758	Dec	24	101	2014–2019	High	10 (High)	1.67	0.54	30.1	5.3	97.84
Rolling Plains													
1	Shackelford, Haskell	4,063	Jan	21	111	2016–2020	Low	3 (Low)	0.62	0.27	45.9	5.5	89.94
2	Kent	4,039	Jan	19	109–111	2016–2020	Low	3 (Low)	0.72	0.30	34.0	2.8	98.52
3	Fisher	1,910	Jan	9	51–54	2016–2020	High	10 (High)	1.76	0.74	38.0	5.6	74.83
4	Scurry	2,323	Jan	17	62–66	2016–2020	High	10 (High)	0.87	0.41	35.5	4.0	68.00

Soils on our study sites included clay loams to loamy sands. Common soil series included Miles (fine-loamy, mixed, superactive, thermic Typic Paleustalfs) and Nobscot (loamy, mixed, superactive, thermic Arenic Paleustalfs; U.S. Department of Agriculture 2021). Honey mesquite is common across most rangelands in this ecoregion depending on the soil type (Landers 1987). Other widespread brush species include prickly pear (*Opuntia* spp.), lotebush (*Ziziphus obtusifolia*), redberry juniper (*Juniperus pinchotii*), and sand shinnery oak (*Quercus havardii*; Rollins 2007). Typical grasses include sideoats grama (*Bouteloua curtipendula*), silver bluestem (*Bothriochloa saccharoides*), tobosa grass (*Pleuraphis mutica*), and Texas wintergrass (*Nasella leucotricha*; Landers 1987). Dominant fauna include white-tailed deer, wild pigs (*Sus scrofa*), coyotes, and wild turkey.

Study sites were separated by 20–100 km and spanned 5 counties (Fisher, Haskell, Kent, Scurry, Shackelford; Edwards 2019, Ritzell 2020). These sites collectively encompassed 12,335 ha. As was the case for sites in the Rio Grande Plains, habitat-management practices on the sites varied and included cattle grazing, chemical and mechanical brush management, prescribed fire, and discing. Cultural practices on the sites also varied and included supplemental feeding, supplemental water, and predator management. Sites ranged in focus from being mostly working ranches (livestock focus) to recreational ranches (bobwhite focus) and thus exhibited variability in intensity of quail management.

METHODS

We evaluated bobwhite density (response variable) as a function of local rainfall and management intensity (predictor variables). We collected data from 3 general sources: helicopter surveys to estimate bobwhite density, open-source databases to obtain rainfall and land-cover information, and landowner surveys to quantify management intensity. We collected bobwhite density at the site level, rainfall within 7-km buffers from site centroid (resolution = 4 × 4 km), and management intensity at the site level.

Density estimation

We conducted helicopter surveys within a distance-sampling framework (Buckland et al. 2015) to estimate bobwhite density during December 2014–2019 (Rio Grande Plains) and January 2016–2020 (Rolling Plains). Time period between surveys in the Rio Grande Plains and Rolling Plains was only about 2 weeks in any given year. Because the calendar year changed between surveys in the ecoregions, we designated year for the Rolling Plains surveys as the same calendar year as for Rio Grande Plains surveys so that data between ecoregions were appropriately paired in time.

We conducted helicopter surveys following the general protocol of Rusk et al. (2007), Schnupp et al. (2013), and Edwards (2019). We created linear transects for each site using geographic information systems (ArcGIS 10.4.1, Redlands, CA, USA). We spaced transects systematically (200–400 m apart) across any given site to achieve uniform coverage. Transects were oriented either north-south or east-west and flown in an appropriate direction depending on the prevailing winds on the survey date (i.e., perpendicular to prevailing winds to avoid hazardous tailwinds).

We conducted helicopter surveys from 0800 to 1700 using a 4-seat Robinson R44 helicopter (Robinson Helicopter Company, Torrance, CA, USA). The pilot flew transects at a relatively low speed (~37 km/hr) and low altitude (~8 m). The surveys involved a pilot and 3 passengers. The front-seat observer searched for coveys in front of the helicopter, while the 2 back-seat observers searched for coveys on their respective side (left or right) of the helicopter. The pilot served as a fourth observer, noting covey detections when observed. The front-seat observer possessed a Juno 3B handheld global positioning system (GPS; Juno, Trimble Navigation, Sunnyvale, CA, USA) to record size and location of any covey detections using a CyberTracker database (CyberTracker Conservation, Capetown, South Africa).

When observers detected a covey, they notified the pilot, who maneuvered the helicopter into a hover and oriented the helicopter so that the side of the helicopter containing the observer who detected the covey faced the covey location. The observer noted covey size and documented the covey location using a Trimble LaserAce 1000 rangefinder that obtained straight-line distance and horizontal and vertical angles to the covey location. These data were wirelessly transmitted to the Juno-handheld device, which recorded the helicopter's GPS location. The CyberTracker platform used the data collected by the GPS and rangefinder to calculate a geo-referenced location of the covey. Upon survey completion, observers downloaded covey locations from CyberTracker to a geographic information system to calculate the perpendicular distance of each covey to the transect line. This information (covey size, survey length, and perpendicular distance to detections) formed the raw data used to estimate bobwhite density.

We used Program DISTANCE 7.1 to estimate bobwhite density for each site by year following conventional distance sampling methods described in Buckland et al. (2015). We calculated density as:

$$\widehat{D} = \frac{n}{2\hat{\mu}\,L} \times E(s)$$

$$\mathrm{var}(\widehat{D}) = \widehat{D}^2 \times \{[\mathrm{CV}(n)]^2 + [\mathrm{CV}\{f(0)\}]^2\},$$

where $\widehat{D}$ is estimated density, n is number of observed coveys, $\hat{\mu}$ approximates effective half-width, L is transect length, $E(s)$ is the mean covey size, CV is the coefficient of variation, and $f(0)$ is the probability density function evaluated at zero distance.

We fit uniform, half-normal, and hazard-rate key functions that were individually adjusted with cosine, Hermite polynomial, and simple polynomial series, respectively (6 models). We determined a right truncation distance based on the distance where the modeled detection function equaled $g(w) = 0.1$ (Williams and Thomas 2007) and identified best-fit models based on absolute and relative model fit. We used Kolmorogov-Smirnov and Cramer VonMises test to evaluate absolute fit and used Akaike's Information Criterion (AIC) to assess relative fit. We only considered models with absolute fit measures $P > 0.05$ and minimum AIC values (ΔAIC < 2.00; Burnham and Anderson 2000). We calculated final density and variability estimates in Program DISTANCE (Table S1, available in Supporting Information; Buckland et al. 2015).

Rainfall and land cover data

We used the parameter-elevation regressions on independent slopes model (PRISM; PRISM Climate Group, Oregon State University, http://www.prism.oregonstate.edu/, accessed Nov 2020) data to obtain annual rainfall information for each site. We collected monthly rainfall data for each site within a 7-km-radius buffer of each site's centroid point. We chose a 7-km radius based on documented dispersal of bobwhites up to 6.5 km on similar rangeland habitats (Miller et al. 2017). Thus, we assumed the 7-km buffer contained the majority of each site's bobwhite population in a given year. We calculated seasonal rainfall (Apr–Aug) by summing monthly rainfall over this time period for a given site. We selected this time period given the profound influence that rainfall during this time period has on quail populations in semiarid environments (Tri et al. 2012, Rollins 2019).

We quantified the amount of potential bobwhite habitat surrounding each site by calculating the percent of rangeland within the 7-km buffer for each site. We calculated this metric to verify that similar amounts of bobwhite habitat (i.e., rangeland) occurred within the local landscape surrounding each site. We obtained National Agriculture Imagery Program (NAIP) aerial photography (1-m resolution, natural color) for 2014 from the Texas Natural Resources Information System. We classified land cover within the 7-km area surrounding each site following the general protocol of Mata et al. (2018). We imported and classified all 2014 NAIP imagery from each digital orthophoto quarter quad that occurred within the 7-km buffer. We used Program ERDAS Imagine 2015

(Hexagon, Stockholm, Sweden) to classify imagery using an unsupervised classification technique (Mata et al. 2018). We reclassified output images as rangeland, agriculture, urban, water, and roads. We assessed the accuracy of the image classification using a confusion matrix and 200 points/image (Congalton 1991, Mata et al. 2018). We set an 85% accuracy threshold for all classified images (Mata et al. 2018).

Quail-management intensity

We developed a survey instrument to help quantify intensity of quail management on study sites (Institutional Review Board number 2021-024). The survey consisted of a questionnaire that collected information on land-management practices and a rubric that assigned points to these practices to tabulate a management-intensity score. The survey centered on 3 primary categories: habitat management (cattle grazing, brush management [mechanical, chemical], prescribed fire, and discing), cultural practices (supplemental feeding, supplemental water, predator management), and harvest management. Each management activity conducted by a landowner corresponded to a numerical point value based on its general effect (positive, neutral, negative) on bobwhite abundance given current scientific knowledge. Habitat-management practices received greater weighting than cultural practices (1 point vs. 0.5 points, respectively) because habitat-management practices generally can be applied across larger spatial extents than cultural practices and thus influence a larger proportion of a site's bobwhite population. More importantly, habitat-management practices have been documented to produce positive responses in bobwhite abundance on semiarid rangelands, whereas cultural practices generally have not (Guthery 1997, Brennan 2007). We obtained a score for a given site by summing points across all questions. Scores could range from zero (no quail-favorable practices implemented) to 14 (all quail-favorable practices implemented). Our goal was not to determine an exact management intensity for a given site, a difficult if not impossible task, but rather to be able to assign sites into relative management-intensity categories (i.e., low, medium, and high). We used scores to categorize sites into 3 management-intensity levels: low (0–4 score), moderate (5–9 score), and high (10–14 score). As a separate, independent assessment of management intensity, the questionnaire also contained a question whereby interviewees were asked to self-identify their primary management goal on a continuum from 1 (sole livestock interest) to 10 (sole quail interest). We also used this self-reported score to categorize sites into 3 management-intensity levels: low (1–4 score), medium (5–7 score), and high (8–10 score). We used site categorization based on this self-identified score to compare with the categorization achieved using the rubric and provided an independent check on the appropriateness of a site's assigned management-intensity category.

We refined the survey (i.e., questionnaire, rubric, and interview process) in 2 phases prior to use in data collection. The first phase involved an independent review by a colleague not involved with the research but with extensive experience designing and implementing landowner surveys who reviewed the questionnaire for clarity and objectivity. We then implemented a second phase of evaluation by conducting a pilot test of the survey, which consisted of interviewing 3 land managers not involved with this research but highly experienced in ranching operations and quail management. We conducted mock interviews as per our protocol and after completion refined the survey questionnaire and protocol based on their feedback. We then used this revised survey for actual data collection.

We used the questionnaire to conduct in-person interviews of landowners and-or land managers participating in this research during June–August 2018. Prior to the start of an interview, we informed interviewees that all information was confidential and noted the purpose of the interview was to obtain general information on their land-management practices. Interviews lasted 45–60 minutes. We recorded interviews using an Apple iPhone 8 (Apple, Cupertino, CA, USA) and subsequently transcribed each interview into a Microsoft Word (Microsoft, Redmond, WA, USA) document. We used these Word documents to quantify responses post-interview using the rubric and tabulated a management-intensity score for a given site. We then categorized sites into a management-intensity category (i.e., low, moderate, high) based on site score as defined above.

Statistical analysis

We conducted analyses by ecoregion because of statistical and ecological considerations. Statistically, the dataset was disconnected (Searle 1971, Milliken and Johnson 2009) with respect to tests of management, year, ecoregion, and their interactions. This condition occurred because data consisted of 3 management levels (low, moderate, high) in the Rio Grande Plains and 2 management levels (low, high) in the Rolling Plains. Additionally, we collected data during 2014–2019 in the Rio Grande Plains and 2015–2019 in the Rolling Plains. Hypotheses involving model parameters that correspond to missing treatment combinations generally cannot be tested without making additional assumptions about the missing treatment combination (Milliken and Johnson 2009), and we were unwilling to make such assumptions. Ecologically, the study sites in the Rio Grande Plains and Rolling Plains are separated by more than 650 km. Such long distance results in notable environmental differences between ecoregions in terms of weather (temperature, rainfall, wind, evapotranspiration), landscape (soil type, vegetation, historical disturbances, fragmentation), and bobwhite demography (Hernández et al. 2007, Rollins 2007). Thus, we analyzed ecoregions separately. We use the term ecoregion in a general sense to broadly distinguish between the Rio Grande Plains and Rolling Plains and acknowledge that the number of sites in this study may not adequately characterize these entire ecoregions.

We used a linear mixed model (McCulloch et al. 2008) to test fixed effects of management intensity, year of sampling, their interaction, and seasonal (Apr–Aug) rainfall on mean bobwhite densities for each ecoregion. We modeled site as a random effect nested within management intensity. We used a repeated measures analysis with site nested within management intensity as the subject for modeling the following variance-covariance structures to account for possible temporal non-independence (Fitzmaurice et al. 2011): first-order autoregressive, compound symmetry, and Toeplitz (and their heteroscedastic versions), first-order autoregressive-moving average, variance-components, and unstructured. Compound symmetry models a constant correlation between successive sampling periods and homogeneous variances among sampling periods; this suggests lack of independence that is, however, constant across sampling periods. The Toeplitz structure models the correlation at adjacent sampling periods as constant, and homogeneous variances among sampling periods; thus, the lack of independence depends on the interval between sampling periods. The first-order autoregressive structure models the correlation between sampling periods as with homogeneous variances; thus, the correlation between sampling periods diminishes as function of the interval between periods. Heterogeneous versions of the above are similar with respect to correlation among sampling periods, but they model heterogeneous variances. The variance-components structure assumes independence among sampling periods, and the unstructured patterns assumes non-dependence that is unstructured; patterns of non-independence are neither constant nor a function of interval between sampling periods. Patterns of non-independence need not have a subject-matter justification (Huynh 1978); their use is to account for the lack of independence common in repeated measures and longitudinal data sets, regardless of the reasons that are responsible for the lack of independence so that appropriate standard errors can be estimated and valid inferences can be drawn. Additionally, accounting for lack of independence generally increases the precision with which model parameters can be estimated (Fitzmaurice et al. 2011). We assessed normality of residuals with the Shapiro-Wilk test.

To account for the variability associated with the density estimates produced by Program DISTANCE, we used a weighted analysis with 2 candidate weighting strategies that included as weights the standard deviation or the variance. We chose the weighting scheme that yielded a residual variance closest to 1 (Kutner et al. 2004). We used Satterthwaite's (1946) method to estimate degrees of freedom. We used AIC corrected for sample size (AIC_c) to select the most appropriate combination of weighting and variance-covariance structure (Barnett et al. 2010). For both ecoregions, we weighted by the standard deviation and modeled with the variance-components structure (Table S2, available in Supporting Information). We used a protected least significant difference test to compare means when the *F* test on mean equality was rejected (Smith and Han 1981). We followed Lipsitz et al. (2001) to estimate a partial coefficient of determination for rainfall given management, year, and management × year effects, and management and its interaction with year given rainfall, adhering to the principle of model hierarchy (McCullagh and Nelder 1983, Bien et al. 2013). We estimated *P*-values using a likelihood ratio approach (Lipsitz et al. 2001). We conducted all analyses using SAS/STAT software, version 9.4. (SAS Institute, Cary, NC, USA).

RESULTS

Site characteristics and environmental context

Using the management-intensity rubric, we classified sites as low ($n = 4$ sites), medium ($n = 5$ sites), and high ($n = 2$ sites) management intensity in the Rio Grande Plains (Table 1). The rubric only classified sites as low ($n = 2$ sites) and high ($n = 2$ sites) management intensity in the Rolling Plains. Using the self-reported management score provided by landowners, sites were classified into the same management categories as was determined using the rubric (Table 1). This congruence in site classification based on 2 independent assessments provided evidence that sites had been appropriately assigned into relative management-intensity categories.

Rangeland comprised the majority of the area surrounding study sites in both ecoregions (Table 1). Rangeland cover comprised virtually all (97–99%) of the area surrounding sites in the Rio Grande Plains and a lesser but still majority (68–98%) of the area surrounding sites in the Rolling Plains. Regarding environmental conditions, both ecoregions experienced historical drought (2011) prior to the initiation of this study; however, annual rainfall increased and peaked during the initial phase of this study, and subsequently decreased over time (Figure 2A,B).

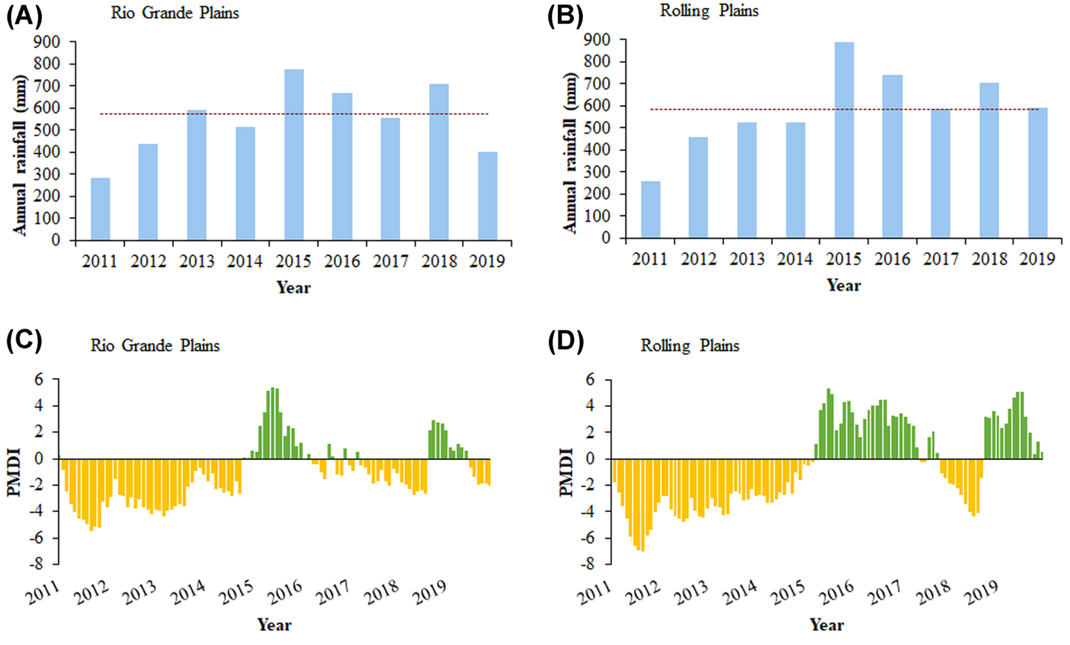

FIGURE 2 Annual rainfall (mm) for the Rio Grande Plains (A) and Rolling Plains (B) of Texas, USA, 2011–2019. Long-term means (1895–2019) for each ecoregion (576 mm and 585 mm, respectively) are indicated by dashed line. Monthly Palmer Modified Drought Index (PMDI) for the Rio Grande Plains (C) and Rolling Plains (D) of Texas, 2011–2019. Rainfall and PMDI data were obtained from the National Climatic Data Center for the Southern Climate Division 9 (Rio Grande Plains) and Low Rolling Plains Climate Division 2 (Rolling Plains) of Texas. The PMDI values range from −6 to 6, with negative values indicating dry conditions (yellow) and positive values indicating wet conditions (green)

Environmental conditions therefore progressed from xeric to mesic and then back to progressively more xeric over the course of the study (Figure 2C,D).

Influence of management and rainfall

Bobwhite populations in the Rio Grande Plains and Rolling Plains experienced a boom-and-bust cycle during this study. This was a fortuitous occurrence given that bobwhite irruptions in semiarid environments occur infrequently (Lusk et al. 2007), and it was important to evaluate the influence of management on quail populations during both poor (drought) and favorable (wet) conditions.

In the Rio Grande Plains, management and year interacted ($F_{10,52.5} = 3.64$, $P < 0.001$) in their effects on bobwhite density (Figure 3). Mean bobwhite density significantly increased with increasing management intensity in 4 of 6 years (Figure 3). We documented a 142–178% increase in mean bobwhite density from low to high management intensity in 2015 (1.12 ± 0.17 bobwhites/ha vs. 2.87 ± 0.39 bobwhites/ha, respectively), 2016 (1.06 ± 0.20 bobwhites/ha vs. 2.96 ± 0.36 bobwhites/ha, respectively), 2017 (0.73 ± 0.16 bobwhites/ha vs. 1.91 ± 0.32 bobwhites/ha, respectively), and 2019 (0.42 ± 0.14 bobwhites/ha vs. 1.01 ± 0.26 bobwhites/ha, respectively). Mean bobwhite density did not differ ($P > 0.169$) among management strategies during the other years (Figure 3). Additionally, bobwhite density differed among years under medium ($F_{5,53.7} = 10.25$, $P < 0.001$) and high ($F_{5,54.1} = 6.75$, $P < 0.001$) management intensity but not low ($F_{5,51.9} = 0.47$, $P > 0.797$) management. A full model with rainfall, management, year, and management × year effects explained 73% ($P < 0.001$) of the variation in bobwhite density. Rainfall at the site level had a positive partial effect ($\hat{\beta} = 0.025 \pm 0.013$) on bobwhite density but accounted for only 9.5% ($P < 0.015$) of the variation in bobwhite density. In contrast, management effects accounted for 64% ($P < 0.001$) of the variation in bobwhite density.

In general, we detected similar trends in the Rolling Plains. Management and year interacted ($F_{4,20} = 5.00$, $P < 0.006$) in their effects on bobwhite density (Figure 4). We detected management effects in 2 of 5 years.

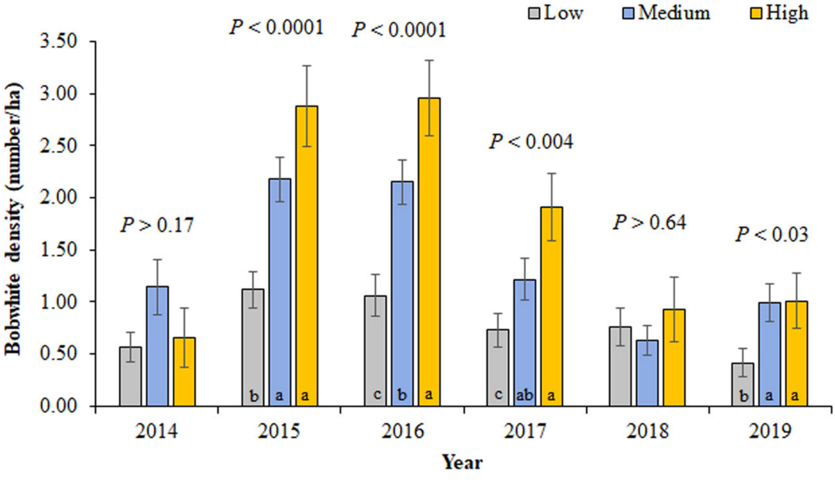

FIGURE 3 Northern bobwhite density ($\bar{x}$ ± SE; number of bobwhites/ha) on sites with low ($n = 4$ sites), medium ($n = 5$ sites), and high ($n = 2$ sites) quail-management intensity in the Rio Grande Plains, Texas, USA, December 2014–2019. We estimated northern bobwhite density using helicopter surveys within a distance sampling framework. Management means are estimated at seasonal (Apr–Aug) rainfall totals for corresponding years via analysis of covariance. Suspended P-values correspond to tests of management effects for corresponding years; management means within a year with same letter are not significantly different (protected least significant difference test)

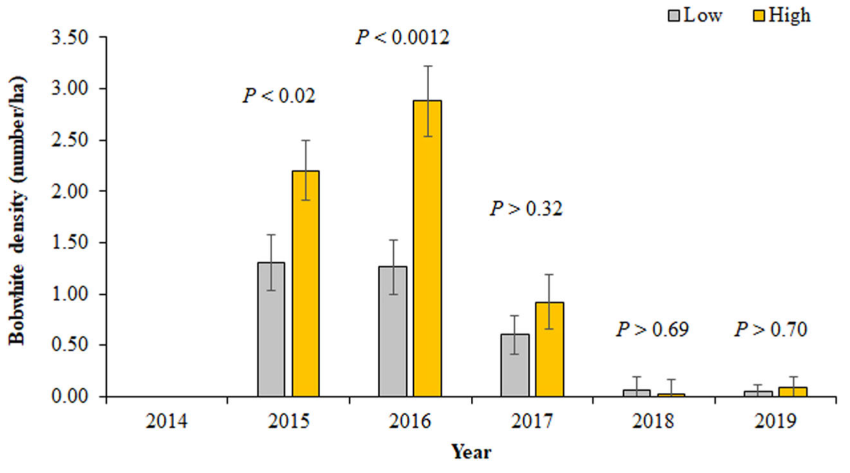

FIGURE 4 Northern bobwhite density ($\bar{x}$ ± SE; number of bobwhites/ha) on sites with low (n = 2 sites) and high (n = 2 sites) quail-management intensity in the Rolling Plains, Texas, USA, December 2015–2019. We estimated northern bobwhite density using helicopter surveys within a distance sampling framework. Management means are estimated at seasonal (Apr–Aug) rainfall totals for corresponding years via analysis of covariance. Suspended P-values correspond to tests of management effects for corresponding years

We documented a 69–129% increase in mean bobwhite density from low to high management intensity in 2015 (1.30 ± 0.27 bobwhites/ha vs. 2.20 ± 0.29 bobwhites/ha, respectively) and 2016 (1.26 ± 0.26 bobwhites/ha vs. 2.88 ± 0.34 bobwhites/ha, respectively). Bobwhite density did not differ ($P > 0.324$) among management strategies during the other years. In addition, mean bobwhite density differed among years under low-intensity ($F_{4,20} = 12.94$, $P < 0.001$) and high-intensity management scenarios ($F_{4,20} = 26.80$, $P < 0.001$). A full model with rainfall, management, year, and management × year accounted for 90.3% ($P < 0.001$) of the variation in bobwhite density. Rainfall at the site level accounted for 0.2% ($\hat{\beta} = -0.002 \pm 0.009, P > 0.826$) of the variation in bobwhite density. In contrast, management effects accounted for 89.6% ($P < 0.001$) of the variation in bobwhite density.

DISCUSSION

We documented that bobwhite density generally increased with increasing management intensity but that bobwhite density continued to fluctuate widely among years independent of management. We also observed that rainfall at the site level accounted for a low amount (<10%) of the variation in bobwhite density, whereas management effects explained 64–89% of the variation in bobwhite density. These results supported our research hypotheses of a general, positive relationship between bobwhite density and management intensity and of a lower influence of rainfall on bobwhite populations at a smaller spatial extent. These results did not support our hypothesis that increasing management intensity would decrease temporal variation in bobwhite density (i.e., that management would stabilize the boom-and-bust cycle).

Several researchers have investigated the response of bobwhites to management throughout the species' geographic distribution. A general pattern is that bobwhite response to management appears to be more consistent in the mesic portion of the species' distribution (eastern USA) than in the more xeric, western portion (southwestern USA). For example, in the northeastern United States, Burger and Linduska (1967) reported that the number of bobwhite coveys increased from 5 to 38 in response to management over a 9-year period on a 1,214-ha farm in Maryland, USA. In the Midwest, Ellis et al. (1969) reported that bobwhite density increased from 0.99 bobwhites/ha to 2.37 bobwhites/ha during a 6-year period in response to management on a 100-ha area in Illinois, USA.

Similarly, in the Southeast, Terhune et al. (2009) reported that, following intensive management, bobwhite populations increased from 0.86 bobwhites/ha to 1.48 bobwhites/ha during a 3.5-year period on a 3,734-ha area in Georgia, USA.

Response of bobwhites to management appears to become less consistent in semiarid environments (or as environmental conditions become more variable). For example, in northwestern Texas, Webb and Guthery (1982) documented that bobwhite density tended to be greater in managed sites (1.3–1.4 bobwhites/ha) than non-managed control sites (0.5–1.1 bobwhites/ha) by the end of their 2-year study. Although bobwhites responded positively to management (1.17–1.80 times increase), bobwhite abundance also exhibited strong increases on the control sites (1.20–1.50 times increase) likely in response to increased rainfall. In southeastern Texas, Kane (1988) documented an immediate but short-term (<1 yr) increase in bobwhite density following management. We documented that, although bobwhite density tended to increase with increasing management intensity, the strength of the response varied by year.

It is unknown exactly what makes one year different from another. Total amount of rainfall certainly is one factor influencing systems in semiarid environments, but years differ in many other respects that involve abiotic and biotic sources of variation. For example, abiotic differences across time could occur in rainfall and in timing and pattern of rainfall (when rainfall is received and how frequently it occurs), and in temperature extremes and duration of temperature fluctuations. Biotic differences among years can occur in habitat conditions (amount of herbaceous cover, food availability) and ecological processes (changes in degree of predation, herbivory, competition, disease). Such interannual variation in environmental conditions can create inconsistent responses to management, and identifying the exact interannual differences that influence a system can be difficult (Stuble et al. 2017). In our study, the effect of management tended to be less evident during dry years (negative Palmer Modified Drought Index) than wet years (positive Palmer Modified Drought Index). Although such a result may question the value of management during drought, the benefit of management may not occur during dry years but rather be expressed during wet years in the form of a more rapid and pronounced population response. Brazil et al. (2012) documented that bobwhite populations responded more strongly on managed sites when conditions improved following drought than on less intensively managed sites. Our data indicated the greatest gains in bobwhite density occurred during regional wet periods in sites with the highest management intensity. This general phenomenon is a concept that has been noted in past literature discussing accidental versus purposeful management (Guthery and Brennan 2007, Larson et al. 2010).

We observed that rainfall at the site level explained considerably less (<10%) of the variation in bobwhite density than past studies have documented for rainfall at a regional level. Recently, Hernández (2020) suggested that the influence of rainfall on bobwhite abundance may decrease with decreasing spatial extent based on hierarchy theory (Allen and Star 1982). Hierarchy theory proposes that systems are structured in nested levels that result in a constraint envelope, whereby the dynamics of an ecological system operate within the limitations imposed by the environmental limits of higher levels and the biotic potential of lower levels (O'Neill et al. 1989, Wu 2013). An important deduction arising from hierarchy theory is that a variable that accounts for most of the variation in a pattern at a large scale will inherently account for less of the variation at a smaller scale because other variables assume importance (Meentemeyer and Box 1987, Sala et al. 1988). Interpreting past research on the bobwhite-rainfall relationship within a hierarchical framework (and with a consideration for scale) supports this prediction of a decreasing influence of rainfall with a decreasing spatial extent (Hernández 2020). Our study provides additional evidence in support of this general pattern.

Collectively, our results and those of past researchers suggest that, in semiarid rangelands, rainfall may provide a broad-scale environmental context within which bobwhite populations operate but may represent only 1 of a suite of local factors influencing abundance at smaller spatial extents. That is, rainfall may be exerting a strong influence on regional abundance—elevating or depressing abundance at broad spatial extents—while local abundance may vary spatially within these general bounds as local factors (of which rainfall is 1) change across space. Such a proposed hierarchical framework for understanding the influence of rainfall on bobwhite populations in semiarid environments (Hernández 2020) is similar to that proposed for other systems, whereby coarse-grain patterns constrain fine-scale processes, but variability at the fine scale is influenced by factors operating at this fine scale plus those operating at the coarse scale (Sala et al. 1988, Fuhlendorf et al. 2017).

The response of bobwhites to management appeared stronger in the Rio Grande Plains than in the Rolling Plains. This finding may be related to the relatively shorter time series and fewer study sites in the Rolling Plains, both of which could have affected statistical power. Bobwhite density also tended to be lower in the Rolling Plains, and it is possible that the fewer detections (and thus more variable density estimates) may have limited the ability of our analyses to detect a significant difference. From an ecological perspective, it is possible that bobwhites may be exhibiting a more muted response to management in the Rolling Plains because they inhabit a more fragmented landscape. In our study, the percent of rangeland surrounding sites in the Rolling Plains was lower (68–98%) than in the Rio Grande Plains (97–99%) thereby indicating less rangeland in the former. Fuhlendorf et al. (2017) proposed that broad-scale patterns of habitat had to be suitable for prairie grouse (*Tympanuchus* spp.) before success could be achieved by fine-scale management. Our findings in the Rolling Plains may reflect such a circumstance (Hernández 2021).

Quail management on our study sites consisted of a variety of habitat-management (e.g., cattle grazing, prescribed fire, brush management) and cultural practices (e.g., supplemental feeding, supplemental water). Because sites possessed unique combinations of quail-management practices, bobwhite density was a response to the collective influence of these practices and could not be attributed to any single practice. Effective bobwhite management in semiarid rangelands therefore may involve a collective approach to management that consists of a suite of practices and may not hinge on the discovery of a single best management practice as traditionally has been the approach (Brennan 2007). Such a change in perspective from a reductionist strategy to a holistic approach recently has been proposed in nutrition science, where evaluation of the value of food as a whole, rather than individual nutrients, may be a more productive and effective approach for enhancing health and advancing science (Jacobs and Tapsell 2007, Provenza et al. 2015). Perhaps quail management in semiarid rangelands also could benefit from such a shift in perspective.

MANAGEMENT IMPLICATIONS

Our research suggests that management can increase bobwhite density beyond that of less intensively managed properties in semiarid rangelands and that rainfall appears to exert a lesser influence on bobwhite density at small spatial extents (e.g., 2,000 ha) than has been documented at large spatial extents (e.g., 8 million ha). However, management may not be able to eliminate inter-annual population fluctuations. Quail management in our study consisted of unique combinations of habitat-management and cultural practices. Landowners interested in bobwhite management in semiarid rangelands may have to use a collective approach to management that consists of a suite of practices rather than pursuing the discovery of a single best management practice.

ACKNOWLEDGMENTS

This manuscript is Caesar Kleberg Wildlife Research Institute Publication Number 21–105 and East Foundation Manuscript Number 063. On 9 March 2020, A. D. Ritzell passed away after a brief but hard fought battle against glioblastoma. A. D. Ritzell was a student, colleague, and dear friend to many of us. He collected these data as part of his research for his Master of Science and greatly contributed to the writing of this manuscript prior to his death. T. A. Campbell, A. M. Foley, and D. G. Hewitt provided constructive comments on an earlier version of this manuscript. Cooperative funding for this research was provided by Reversing the Quail Decline Initiative (Texas AgriLife), Texas Parks and Wildlife Department, South Texas Chapter of the Texas Quail Coalition, and East Foundation. A. D. Ritzell was supported by the Hixon Endowed Fellowship in Quail Research and the René Barrientos Tuition Assistance Program at Texas A&M University-Kingsville, and by the Houston Safari Club International Graduate Scholarship. F. Hernández and L. A. Brennan were supported by the Alfred C. Glassell Jr.

Endowed Professorship and C.C. Winn Endowed Chair for Quail Research, respectively, in the R. M. Kleberg, Jr. Center for Quail Research at Texas A&M University-Kingsville. D. Rollins was supported by the Rolling Plains Quail Research Foundation.

CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

ETHICS STATEMENT

This research was conducted under the auspices of the Institutional Animal Care and Use Committee at Texas A&M University-Kingsville (Institutional Review Board number 2021-024) and followed the ethical treatment of birds as outlined by the North American Ornithological Council.

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Associate Editor: Anthony Roberts.

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How to cite this article: Ritzell, A. D., F. Hernández, J. T. Edwards, A. Montalvo, D. B. Wester, E. D. Grahmann, D. Rollins, K. G. Stewart, R. A. Smith, D. A. Woodard, and L. A. Brennan. 2022. Quail and rain in semiarid rangelands: does management matter? Journal of Wildlife Management e22209. https://doi.org/10.1002/jwmg.22209