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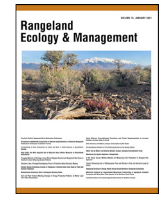

Diverse, Native-Plant Communities as Important Nesting Habitat for Chestnut-Bellied Scaled Quail☆

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ABSTRACT

Habitat loss and fragmentation have been implicated in the decline of chestnut-bellied scaled quail (*Callipepla squamata castanogastris*) in southern Texas, U.S.A. Although a general affinity of the subspecies for native thornscrub is known, its specific habitat requirements are less studied, and no information exists regarding its demography. We conducted a study in southern Texas ($n = 5$ ranches; LaSalle and McMullen counties) to 1) quantify survival, reproduction, and occupancy of chestnut-bellied scaled quail and 2) characterize its nesting habitat to help inform future rangeland management. We captured and radio-collared individuals ($n = 137$) during Mar–Aug 2013 and 2014 to estimate survival and reproduction and conducted call-count surveys ($n = 60$ points) during May–August of both years to estimate occupancy and detection probability. We measured vegetation characteristics at nest sites ($n = 53$ nests) and paired random points to document habitat use. We documented seasonal survival (0.68–0.85), clutch size (10–11 eggs), and apparent nest success (38–59%) that were within values reported for scaled quail in other portions of its geographic distribution. However, relative abundance was low (0.14–0.25 calling males/point), as was occupancy (0.56–0.73) and probability of detection (0.10–0.32). Regarding nesting habitat, pricklypear (*Opuntia engelmannii* Salm-Dyck ex Engelm.) was the most common nesting substrate (68%; $n = 53$ nests), with pricklypear (95% CI $\beta = 0.992–1.105$; $P < 0.09$), woody plants (95% CI $\beta = 1.001–1.042$; $P < 0.04$), and native grasses (95% CI $\beta = 0.993–1.129$; $P < 0.08$) being important variables distinguishing nests from random sites. Nest survival was negatively influenced by non-native grass cover (95% CI $\beta =$ -0.115 to -0.006). Preservation of diverse shrub and native-grass communities should receive high consideration when planning brush management in southern Texas if conservation of chestnut-bellied scaled quail is a goal.

Introduction

The chestnut-bellied scaled quail (*Callipepla squamata castanogastris*) is a subspecies of scaled quail that inhabits thornscrub communities in southern Texas, U.S.A. and northern Mexico (Brennan et al., 2017). Although scaled quail populations fluctuate considerably from year-to-year in response to rainfall (Campbell 1968; Bridges et al., 2001), the species has experienced considerable population declines across its geographic distribution (Church et al., 1993). According to Breeding Bird Survey, scaled quail have declined 2% per year in the U.S. during 1967–2021, with chestnut-bellied scaled quail declining about twice this rate (4% per year) during the same period (Sauer et al., 2020). Various factors have been proposed as causes of the scaled quail decline including habi-

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tat loss and fragmentation (Silvy et al., 2007; Rho et al., 2015), disease (Rollins, 2000), and predators (Rollins and Carroll, 2001).

Unlike the more northern and western subspecies of scaled quail that inhabit open grasslands with low shrub cover, chestnut-bellied scaled quail inhabit dense, multi-canopied thornscrub possessing sparse herbaceous understory (Reid et al., 1979; Hammerquist-Wilson and Crawford, 1987). The subspecies uses areas with moderate to high amounts of woody cover (>35%), low grass cover (10–25%), and high bare ground (70–80%) (Hammerquist-Wilson and Crawford, 1987; Fulbright et al., 2019). Chestnut-bellied scaled quail appear to be particularly sensitive to invasive, non-native grasses (Fulbright et al., 2019) and tend to favor undisturbed, native-plant communities (Hernández et al., 2025). Anecdotal evidence suggests that pricklypear (*Opuntia* spp.) may be an important component of their habitat given that abundance of chestnut-bellied scaled quail is associated with areas of dense pricklypear (Lehmann and Ward, 1941).

The habitat affinity of chestnut-bellied scaled quail for dense thornscrub with a sparse herbaceous understory makes the subspecies vulnerable to rangeland management practices that dramatically alter plant communities (Brennan et al., 2017; Hernández et al., 2025). During the past 50–85 yr, the rangelands of southern Texas have been subject to extensive brush management such as root plowing, rollerchopping, aeration, and chaining (Hamilton et al., 2004). The region also has experienced a proliferation of invasive, non-native grasses such as buffelgrass (*Pennisetum ciliare* [L.] Link), Lehmann lovegrass (*Eragrostis lehmanniana* Nees), and Old World bluestems (e.g., *Dichanthium annulatum* [Forssk.] Stapf) (Fulbright et al., 2013a). Of the various brush management practices, root plowing may be the most detrimental to chestnut-bellied scaled quail because it causes severe soil disturbance (Scifres, 1980) and induces a transition in the plant community from a diverse mixed-brush community (20–30 species) to a species poor vegetation state (1–2 fabaceous shrub species) (Stewart et al., 1997; Fulbright et al., 2013b). This new plant community does not return to the prior state even after 30–40 yr (Ruthven et al., 1993; Nolte et al., 1994; Fulbright and Beasom, 1987; Stewart et al., 1997). Root-plowed areas also generally are dominated by non-native grasses, whether due to intentional seeding following root plowing (Ball, 1964) or because of natural invasion into disturbed soil, and are transformed from sparsely vegetated areas to dense, monotypic stands of non-native grass that are well known to negatively impact quails (Flanders et al., 2006; Sands et al., 2009; Fulbright et al., 2013b; Edwards et al., 2022). These large-scale changes have resulted in novel landscapes (Hobbs et al., 2009) that represent alternative stable states (Westoby et al., 1989) and are hypothesized to negatively impact chestnut-bellied scaled quail (Hernández et al., 2012; Hernández et al., 2025).

Although the general habitat affinity of chestnut-bellied scaled quail is known, its specific habitat requirements are less documented. Few studies have investigated its habitat needs (Reid et al., 1979; Hammerquist-Wilson and Crawford, 1987; Fulbright et al., 2019), and no study to date has provided basic information on its demography. We conducted a study in southern Texas to 1) quantify survival, reproduction, and occupancy of chestnut-bellied scaled quail and 2) characterize their nesting habitat to help inform future rangeland management. We hypothesized that the demography of chestnut-bellied scaled quail would fluctuate in response to environmental conditions but exhibit vital rates lower than those reported in other portions of the species' distribution given the chestnut-bellied scaled quail's greater rate of decline. We also hypothesized that chestnut-bellied scaled quail would nest in locations possessing a more diverse shrub community and lower non-native grass cover than available on the landscape.

Methods

Study area

Our study was conducted in the Rio Grande Plains ecoregion of Texas, U.S.A. (Gould, 1960) on five ranches (Altito-Storey Ranch, Hixon Ranch, Golondrina Ranch, Harle Ranch, and Nueces Ranch) separated by 10–40 km and located in LaSalle and McMullen Counties. The study area encompassed 6 104 ha that were comprised of a 1 295-ha area of the Altito-Storey Ranch, a 545-ha area of the Hixon Ranch, an 888-ha area of the La Golondrina Ranch, a 526-ha area of the Harle Ranch, and a 2 850-ha area of the Nueces Ranch. We collected data across multiple ranches to capture spatial representation of the habitat of chestnut-bellied scaled quail.

The Rio Grande Plains ecoregion comprises approximately 8.5 million ha of rolling topography that ranges from 0 m at the coast to approximately 300 m in the northwestern portion of the ecoregion (Correll and Johnston, 1979). It is characterized by a semi-arid, sub-tropical climate that possesses periods of extreme fluctuations in precipitation and temperature. 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 on the study sites were typical of the mixed-brush communities characterizing the ecoregion. Common woody plants and subshrubs on the study sites included mesquite (*Prosopis glandulosa* Torr.), blackbrush (*Vachellia rigidula* (Benth.) Seigler and Ebinger), twisted acacia (*Vachellia schaffneri* (S. Watson) Seigler and Ebinger), guajillo (*Acacia berlandieri* Benth.), brasil (*Condalia hookeri* M.C. Johnst. var. hookeri), cenizo (*Leucophyllum frutescens* [Berl.] I. M. Johnst.), granjeno (*Celtis ehrenbergiana* [Klotzsch] Liebm.), guayacan (*Guaiacum angustifolium* Engelm.), lotebush (*Ziziphus obtusifolia* [Hook. ex Torr. and A. Gray] A. Gray), allthorn (*Koeberlinia spinosa* Zucc.), knifeleaf condalia (*Condalia spathulate* A. Gray), amargosa (*Castela texana* [Torr. and A. Gray] Rose), coma (*Sideroxylon celastrinum* [Kunth] T.D. Penn.), shrubby blue sage (*Salvia ballotiflora* Benth.), Texas persimmon (*Diospyros texana* Scheele), Texas pricklypear (*Opuntia engelmannii* Salm-Dyck ex Engelm.), strawberry cactus (*Echinocereus enneacanthus* Engelm.), and tasajillo (*Cylindropuntia leptocaulis* [DC.] F.M. Knuth). Common native grasses included hooded windmill grass (*Chloris cucullata* Bisch.), Hall's panicum (*Panicum hallii*), curlymesquite (*Hilaria belangeri* [Steud.] Nash), buffalograss (*Buchloe dactyloides*), Texas grama (*Bouteloua rigidiseta* [Steud.] Hitchc.), and several species of bristlegrass (*Setaria* spp.), tridens (*Tridens* spp.), pappusgrasses (*Pappophorum* spp.), and threeawns (*Aristida* spp.). Non-native grasses included buffelgrass (*Pennisetum ciliare* [L.] Link), yellow bluestem (*Bothriochloa ischaemum* [L.] Keng), Kleberg bluestem (*Dichanthium annulatum* [Forssk.] Stapf), Lehmann lovegrass (*Eragrostis lehmanniana* Nees), Mediterranean lovegrass (*Eragrostis barrelieri* Daveau), and Bermudagrass (*Cynodon dactylon* [L.] Pers.). Soils were Bristol, Brundage, Poteet, Duval, and Claid very fine sandy loam; Zavco sandy clay loam; Moglia, Bookout, and Cotulla clay loam; and Chochina, Coquat, and LaSalle clay (NRCS Web Soil Survey, 2012). Livestock grazing occurred on all sites (5–20 ha/AU), and brush management within and among ranches varied from minimal (only brush clearing resulting from energy pipelines) to extensive (multiple practices either single or in tandem). Brush management practices on the ranches included mechanical (e.g., roller chopping, root plowing, shredding), chemical (aerial and individual plant treatment), and prescribed fire.

Population monitoring

We captured chestnut-bellied scaled quail using standard funnel traps baited with sorghum (*Sorghum bicolor* [L.] Moench) during March–August of 2013 and 2014. We established trap sites by creating a grid (10-ha grid cells) using ArcGIS 10.1 to systematically trap quail across sites. We overlaid the grid onto study sites and selected a trap site within each grid cell. Funnel traps were placed under dense-canopied shrubs and checked every 2–3 h beginning at sunrise. We fitted individuals weighing >150 g with a 6–7 g neck-loop radio transmitter (American Wildlife Materials, Monticello, FL, USA) and an aluminum leg band. Our target was to monitor a total of 60 chestnut-bellied scaled quail (40 females and 20 males) per year and to trap as needed during each year to maintain sample size. We preferentially collared females (2 females for every 1 male) to facilitate location of nests and radio-collared ≤ 3 individuals per trap to maximize monitoring of quail across space. This study was approved by Texas A&M University-Kingsville Institutional Animal Care and Use Committee, approval number 2013-02-12B-A1.

We monitored chestnut-bellied scaled quail via radiotelemetry 3–4 times per week using a three-element yagi antenna and a hand-held receiver (Advanced Telemetry Systems, Isanti, MN, USA) to document survival and locate nests. We assumed that a radio-collared bird was nesting if we found it in the same location for >2 consecutive days (Burger et al., 1995b). Once nest incubation was confirmed, we estimated the nest location via triangulation from >10 m away. We continued monitoring the incubating bird from afar (>20 m) until the nest hatched, or the quail was no longer found at the nest site, at which time we approached the nest to record data. We documented nest fate, clutch size, and vegetation characteristics (described below) for all nests.

We conducted call counts (Hansen and Guthery, 2001) during May—August 2013 and 2014 to document relative abundance (no. calling males/point), occupancy, and detection probability. We established survey points by creating a 1-km × 1-km grid in ArcGIS 10.1 and overlaying it on study sites. We used grid points to denote location of survey points ($n = 60$ total survey points). We used a 1-km × 1-km grid to minimize the likelihood of double-counting calling individuals (DeMaso et al., 1992, Rusk et al., 2009). Surveys were conducted approximately once a week (every 7–10 d) during morning hours (06:30–11:00 h) and on days with clear conditions (Hansen and Guthery, 2001). During each survey, we listened for 5 min and recorded the number of calling males. Each survey point was surveyed 14 times during May—August 2013 and 2014.

We obtained monthly values of Modified Palmer Drought Severity Index (PMDI; Palmer, 1965; Heddinghaus and Sabol, 1991) from the National Centers for Environmental Information to characterize environmental conditions prior, during, and after our study (2012–2015). The PMDI incorporates several weather variables (e.g., precipitation, temperature, soil moisture, etc.) into a single metric and can range from ≤ –4 (extreme drought) to ≥ 4 (extremely wet) (Alley, 1984). We calculated mean PMDI for each year and used this information to provide an environmental context for interpreting demographic performance of chestnut-bellied scaled quail.

Vegetation sampling

We measured vegetation at nest sites and paired, random points to document habitat use of chestnut-bellied scaled quail. Random points were established in a random direction (0–359°) and random distance (50–100 m) from nest sites. At each point (nest or random), we used a Daubenmire frame (20 × 50-cm; Daubenmire, 1959) placed at the point and 4 m away in each cardinal direction ($n = 5$ total frames/point) to measure herbaceous cover. At each Daubenmire frame, we visually estimated percent cover of bare ground, litter, and herbaceous plants by species. We used this latter information to calculate percent cover of native grass and non-native grass. We used a profile board (Nudds, 1977) centered at the nest or random point and estimated visual obstruction of the 0–20 cm stratum from a kneeling position (0.5 m height) and 4 m away in each of the cardinal directions.

We assessed the shrub community using line-intercept methodology (Canfield, 1941). We established a 16-m transect in a randomly selected orientation (either north-south or east-west) over the center of the nest or random point. When a shrub extended over the transect line, we identified the species and recorded the length of the transect intersected by the species. We used these data to calculate pricklypear cover, woody-plant cover, and woody-plant species richness. We also measured pricklypear density at each point type using point-center quarter method (Cottam and Curtis, 1949; Mitchell, 2007). We measured the distance from the nest or random point to the nearest pricklypear in each of the 4 quadrants (northeast, southeast, southwest, and northwest) formed by the N-S and E-W directions. We used these distances to calculate pricklypear density at each point following Mitchell (2007).

Statistical analysis

We calculated spring-summer (15 March–15 August) survival of radiomarked chestnut-bellied scaled quail by year using the staggered-entry Kaplan–Meir estimator (Pollock et al., 1989). Individuals lost to dispersal or radio failure were used to estimate survival up to the day they went missing, upon which time the individuals were censored from the analysis (Pollock et al., 1989). We compared survival distributions between years using a log-rank chi-square test (Pollock et al., 1989, Burger et al., 1995a).

We used call-count data to estimate occupancy (Ψ) and probability of detection (p) in Program Mark (version 7.2; White and Burnham, 1999). We developed five *a priori* models to evaluate the influence of year on occupancy and year and time trend (linear and quadratic) on probability of detection and selected the best model using AIC_c (Supplemental Table 1) (Arnold et al., 2010). We compared calling rate (no. calling males/point) between years using Mann-Whitney Test (Conover, 1999).

We used the nest survival model with a logit link function in Program MARK to assess factors influencing daily nest survival. We modeled nest survival as a function of five variables (year, native-grass cover, non-native grass cover, visual obstruction, and pricklypear cover). We constructed 12 biologically relevant, *a priori* models (Supplemental Table 2) and used Akaike's Information Criterion corrected for small sample size (AIC_c) to select the best model (Burnham and Anderson 2002; Arnold et al., 2010). We estimated nest survival for the incubation period (23 d) by exponentiating daily survival rate of the best model to this time length. We compared nesting rate (no. nests/hen) and mean clutch size between years using Mann-Whitney Test (Conover, 1999).

We used conditional logistic regression for matched pairs to evaluate the influence of vegetation characteristics (pricklypear cover, woody-plant cover, woody-plant species richness, subshrub cover, native-grass cover, non-native grass cover, and bare ground) on nest-site selection (Duchesne et al., 2010). We tested for collinearity among predictor variables using Pearson's correlation coefficient. For variables with a significant and moderate correlation (r >0.35), we selected the most ecologically relevant variable of the pair and removed the other. Nest sites and paired, random points represented matched pairs in the statistical analyses (Kleinbaum et al., 1998). We developed continuous selection functions for variables that were influential in determining relative probability of use to determine habitat-suitability bounds for each

Table 1
Survival, reproduction, and relative abundance of chestnut-bellied scaled quail in southern Texas (LaSalle and McMullen counties), U.S.A., April–August, 2013–2014.

Category	2013			2014			*P*-value
Variable	N	Estimate	SE	N	Estimate	SE	
Survival	66	0.68	0.06	71	0.85	0.07	0.02
Reproduction							
Nesting rate (no. nests/hen)	19	1.26	0.13	21	1.38	0.15	0.58
Clutch size	11	11.45	0.92	26	10.46	0.53	0.70
Apparent nest success (%)	24	37.5	0.10	29	58.6	0.09	0.21
Nest survival rate (daily)	20	0.96	0.01	28	0.97	0.01	NA
Nest survival rate (incubation period)	20	0.37	–	28	0.51	–	NA
Relative Abundance							
Calling rate (no. males calling/point)	60	0.14	0.03	50	0.25	0.03	0.01
Occupancy	60	0.56	0.09	50	0.73	0.07	NA

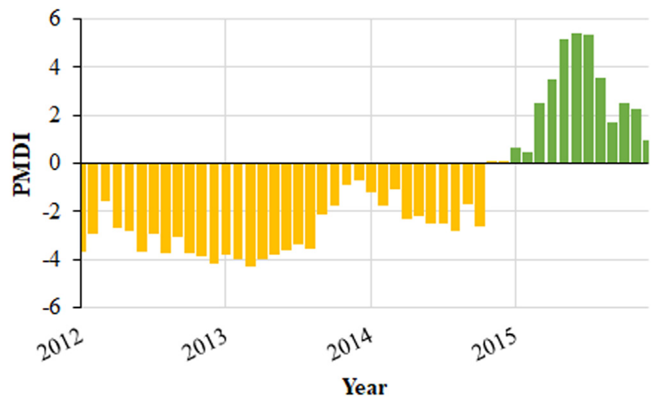

Figure 1. Modified Palmer Drought Severity Index (PMDI) for the Rio Grande Plains of Texas, U.S.A., 2012–2015. Data were obtained from the National Climatic Data Center for the Southern Climate Division 9 (South Texas). The PMDI values range from -6 to 6, with negative values (yellow) indicating dry conditions and positive values (green) indicating wet conditions.

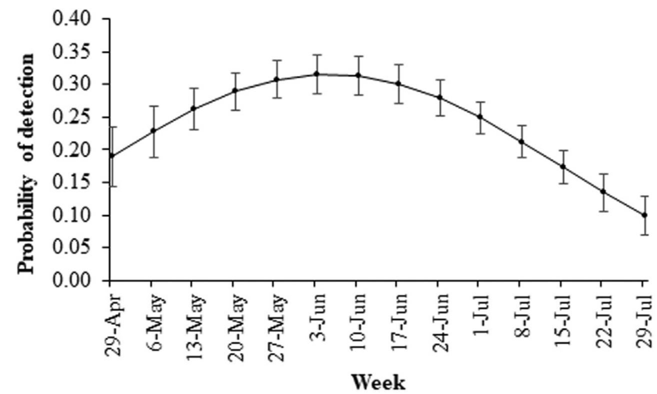

Figure 2. Trend in detection probability of chestnut-bellied scaled quail in southern Texas (LaSalle and McMullen counties), U.S.A., April–August, 2013–2014.

variable (Kopp et al., 1998; Arredondo et al., 2007; DeMaso et al., 2011). We conducted statistical analyses using RStudio (Posit team, 2023) and used an $\alpha = 0.10$ to determine significance (Krausman, 2017).

Results

Basic demography

The Rio Grande Plains experienced drought prior to the initiation of this study (2012). Annual rainfall in the ecoregion began increasing during the next 3 years (2013–2015), and environmental conditions began to transition from xeric to mesic as the study progressed (Fig. 1). Demographic rates of chestnut-bellied scaled quail improved between years, possibly in response to improved environmental conditons (Table 1). Breeding-season survival (Mar–Aug) increased by 25% from 2013 (0.68 ± 0.06) to 2014 (0.85 ± 0.07; $P < 0.02$). Vital rates related to nesting also numerically increased between years such as nesting rate (1.26 nests/hen vs. 1.38 nests/hen), apparent nest success (37.5% vs. 58.6%), and 23-d nest survival (0.37 vs. 0.51) (Table 1). However, the number of renesting attempts did not differ between years ($P < 0.83$). Pooled across years, most hens attempted only 1 nest (75%), with fewer hens attempting two nests (18%) or three nests (7%; $n = 53$ total nests).

This positive population response resulted in relatively higher populations of chestnut-bellied scaled quail during the second year. We documented that the number of calling males increased by 79% from 2013 (0.14 ± 0.03 calling males/point) to 2014 (0.25 ± 0.03 calling males/point; $P < 0.01$). Of the 5 *a priori* models developed to evaluate factors influencing occupancy and detection probability, the most parsimonious model suggested an influence of year on occupancy and a quadratic time trend in detection probability (Supplemental Table 1). Occupancy increased by 30% from 2013 (0.56 ± 0.09) to 2014 (0.73 ± 0.07). Detection probability increased from late April (0.19 ± 0.05) to early June (0.32 ± 0.03), where it peaked and subsequently decreased toward August (0.10 ± 0.03; Fig. 2).

Nesting habitat

Nests generally were located in either a single, primary nesting substrate (i.e., only 1 plant species) or a primary nesting substrate in association with 1–2 secondary plant species. Regarding primary nesting substrate, most nests ($n = 53$) were located in pricklypear (68%) followed by shrubs (21%), grasses (9%), and forbs (2%). Pricklypear that was used as nesting substrate was robust and of moderate height (0.84 ± 0.07 m) and width (2.3 ± 0.34 m). Other species used as primary nesting substrates included cenizo, lotebush, granjeno, twisted acacia, and Texas persimmon for shrubs, and plains bristlegrass (*Setaria leucopila* [Scribn. & Merr.] K. Schum.) and whiplash pappusgrass (*Pappophorum vaginatum* Buckley) for grasses.

We documented that pricklypear density was considerably greater at nests (333.9 plants/ha) than random points (83.8 plants/ha), which resulted in nest sites possessing about twice the amount of pricklypear cover (19.2 ± 2.8%) than was randomly available (8.0 ± 1.9%; $P < 0.001$). Woody cover also was greater at nests (64.8 ± 4.9%) than random points (36.4 ± 4.2%; $P < 0.0001$). The woody cover associated with nest sites contained greater species richness (5.2 ± 0.2 species) than random sites (4.2 ± 0.3 species; $P < 0.003$). These structural characteristics resulted in nests possessing about twice the amount of visual obstruction (54.9 ± 2.7%) than random sites (25.5 ± 3.3%; $P < 0.001$). In contrast, nest sites contained less bare ground (33.5 ± 2.3%) than random sites (49.0 ± 3.0; $P < 0.0003$). We documented no differences

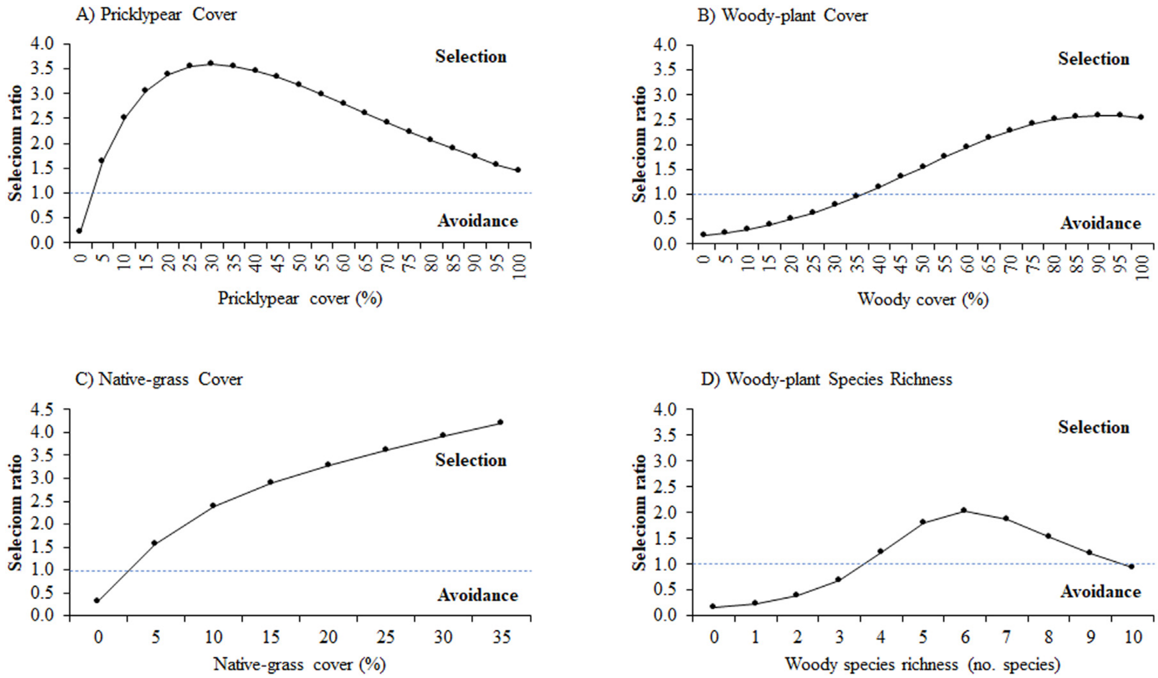

Figure 3. Continuous selection functions for (A) pricklypear cover, (B) woody-plant cover, (C) native-grass cover, and (D) woody-plant species richness at nests ($n = 53$) of chestnut-bellied scaled quail in southern Texas (LaSalle and McMullen counties), U.S.A., April–August 2013–2014.

Table 2
Vegetation characteristics of chestnut-bellied scaled quail nests and paired random points in southern Texas (LaSalle and McMullen counties), U.S.A., April–August, 2013–2014.

Method	Nest			Random			*P*-value
Variable	N	Mean	SE	N	Mean	SE	
Daubenmire frame							
Bare ground (%)	53	33.54	2.33	53	49.00	2.96	0.0003
Native grass cover (%)	53	9.2	1.4	53	7.3	1.5	0.1848
Non-native grass cover (%)	53	2.1	0.8	53	6.4	1.9	0.2515
Profile board							
Visual obstruction (%)	53	54.9	2.7	53	25.5	3.3	0.0001
Point-center quarter							
Pricklypear density (no./ha)	53	339.0	–	53	83.8	–	NA
Line Intercept							
Pricklypear cover (%)	53	19.2	2.8	53	8.0	1.9	0.0014
Shubshrub cover (%)	53	4.4	1.5	53	5.6	2.0	0.6465
Woody cover (%)	53	64.8	4.9	53	36.4	4.2	0.0001
Woody species richness	53	5.2	0.2	53	4.2	0.3	0.0031

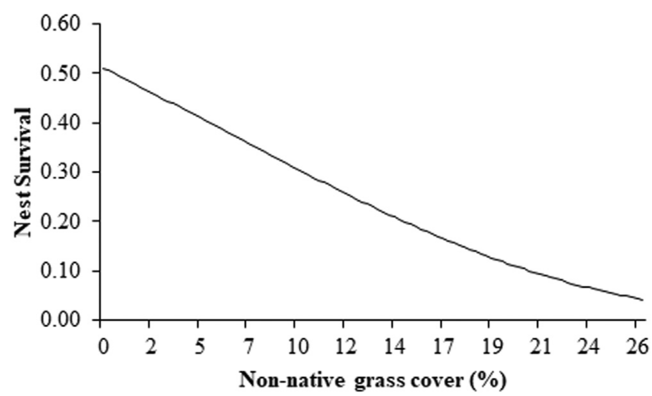

Figure 4. Relationship between non-native grass cover (%) and 23-d nest survival ($n = 53$ nests) of chestnut-bellied scaled quail in southern Texas (LaSalle and McMullen counties), U.S.A., April–August 2013–2014.

in percent cover of native and non-native grasses between nest and random sites, although nests tended to have slightly greater numerical cover of native grasses (Table 2).

We documented that cover of woody plants (95% CI $\beta = 1.001$–1.042; $P < 0.04$), pricklypear (95% CI $\beta = 0.992$–1.105; $P < 0.09$), and native grasses (95% CI $\beta = 0.993$–1.129; $P < 0.08$) were important variables distinguishing nests from random sites. For every 1 unit increase (i.e., 1%) in one of these variables (while holding the others constant), the odds of a site being classified as a nest increased by 2.2% for woody plants, 4.7% for pricklypear, and 5.7% for native grasses. Based on continuous selection functions, chestnut-bellied scaled quail selected nest sites in areas with ≥ 40% woody plant, ≥ 5% pricklypear, and ≥ 5% native-grass cover (Figs. 3A–3C). Chestnut-bellied scaled quail also selected nest sites in areas with a relative high species richness (5–10 species) of woody plants (Fig. 3D). Of the 12 *a priori* models evaluating the influence of nest habitat on nest survival, the most parsimonious model indicated a negative influence of non-native grass (Supplemental Table 2). Nest survival decreased with increasing cover of non-native grass (Fig. 4). Collectively, we documented that nests of chestnut-bellied scaled quail tended to be located in areas characterized by high pricklypear cover, high woody-plant cover and species richness, more native grass cover, and moderate amounts of bare ground than available on the landscape.

Discussion

Our findings broadly supported the research hypotheses. We documented that demographic performance of chestnut-bellied scaled quail fluctuated, likely in response to environmental conditions, and that nesting habitat was characterized by greater and more diverse woody cover than available. We also documented that the likelihood of a location serving as a potential nesting site increased with increasing cover of prickly pear and native grasses. In contrast to expectations, however, the vital rates of chestnut-bellied scaled quail documented during our study were not lower than those reported by past studies in other regions of the scaled quail's distribution.

We documented relatively high spring-summer survival (0.68–0.85) during the 2-yr study. These survival estimates are similar to those documented for scaled quail in western Texas (0.46–0.82) (Rollins et al., 2006; Gonzalez-Gonzalez et al., 2017), northern Texas (0.38–0.80) (Pleasant et al., 2006), and New Mexico (0.22–0.48) (Rollins et al., 2006). Clutch size (10–11 eggs) also was within demographic expectations of the species (10–13 eggs) (Dabbert et al. 2020), as was apparent nest success (38–59%) compared to past studies (44–73%) (Pleasant et al., 2006; Gonzalez-Gonzalez et al., 2017). Relative abundance, however, was much lower (0.14–0.25 calling males/point) than that documented in Arizona (1.5–3.2 calling males/point) (Brown et al., 1978) and other regions of Texas (0.3–2.6 calling males/point) (Rollins, 2017). We documented a low probability of detection (0.10–0.32) during call counts, with peak calling occurring during early-mid June. These observations, coupled with moderate occupancy (0.56–0.73), suggest that the population of chestnut-bellied scaled quail in southern Texas may exist as pockets of occupation on the landscape but in low relative abundance where they occur. Given that survival and reproduction of chestnut-bellied scaled quail appear to be within the range of the species, it is unclear what vital rate(s) may be contributing to the subspecies higher population decline. Low recruitment of young into the population may be one possibility. We note, however, that environmental conditions were transitioning from xeric to mesic during our study. Given the profound positive influence that rain has on southwestern quail populations (Campbell, 1968; Kiel, 1976; Brown, 1989; Bridges et al., 2001; Ritzell et al., 2022), it is plausible that improved environmental conditions during the study may have resulted in demographic estimates than may not be characteristic of the subspecies over a longer term.

We documented that diverse woody-plant cover, pricklypear, and native grasses were important components of nesting habitat for chestnut-bellied scaled quail. Recent research has documented the value of a diverse woody-plant community for general space use by chestnut-bellied scaled quail (Fulbright et al., 2019), and our study extends this general importance to nesting habitat. We observed that chestnut-bellied scaled quail located nests not only in areas of high woody cover (65%) but also selected for nest sites with high woody-plant diversity (5–10 species). Pricklypear appeared to be a valuable component of this nesting habitat. Approximately 70% of nests were located in pricklypear. In addition, nest sites were located in areas with about twice the cover and four times the density of pricklypear than the surrounding landscape. The association between chestnut-bellied scaled quail and pricklypear has been suggested (Lehmann and Ward, 1941), but the importance of pricklypear as a nesting substrate has not. High use of pricklypear as nesting substrate has been observed in northern bobwhite (*Colinus virginianus*) in the Rolling Plains of Texas and is thought to serve as a nest-predator deterrent (Slater et al., 2001; Hernández et al., 2003). It is plausible that chestnut-bellied scaled quail may be nesting in pricklypear for similar reasons (Carter et al., 2002).

An interesting observation is that nest survival of chestnut-bellied scaled quail decreased with increasing cover of non-native grasses. The mechanisms producing this potential negative relationship are unknown, but it could represent a process through which landscape changes trending toward less native and more non-native grasses may be negatively influencing the demography of the subspecies. What is clear is that non-native grasses negatively influence space use of chestnut-bellied scaled quail. The subspecies strongly avoids areas dominated by non-native grass cover (Fulbright et al., 2019). In our study, the odds of a location being a suitable nest site increased by about 6% for every unit increase in native-grass cover. In addition, chestnut-bellied scaled quail selected areas for nesting with >5% native-grass cover.

Collectively, the habitat of chestnut-bellied scaled quail may be broadly described as thornscrub community with sparse herbaceous understory. However, three specific characteristics of the plant community that appear to be important are high diversity (woody and herbaceous), structural complexity, and native origin (Hammerquist-Wilson and Crawford; Brennan et al., 2017; Fulbright et al., 2019; Hernández et al. 2025). In southern Texas, plant communities possessing these characteristics tend to be communities that have not been subject to past, severe disturbances. Based on this knowledge foundation, we propose a *disturbance-based, novel landscape hypothesis* regarding the decline of chestnut-bellied scaled quail. We hypothesize that intensive brush management in southern Texas during the past 50–85 yr —specifically, extensive root plowing of native thorn-scrub followed by planting with non-native grasses—has created novel landscapes (Hobbs et al., 2009) and alternative stable states (Westoby et al., 1989) that have decreased the amount and connectivity of chestnut-bellied scaled quail habitat and contributed to the subspecies' decline at both local and regional scales. Locally, the plant community has been transformed from diverse thornscrub to a simplified, mesquite shrubland dominated by non-native grasses. Regionally, the amount and connectivity of habitat has decreased, altering the landscape pattern of habitat from large, contiguous tracts to small, isolated fragments. If this *disturbance-based, novel landscape hypothesis* is valid, then two predictions arise: 1) locally, areas subjected to intense past disturbance (e.g., root plowing and seeding with non-native grasses) should possess no or a low abundance of chestnut-bellied scaled quail and 2) regionally, populations of the subspecies inhabiting landscapes with greater amount and connectivity of habitat (i.e., undisturbed thornscrub) should exhibit higher demographic performance (e.g., survival, reproduction, abundance, and-or population growth) than those inhabiting more fragmented landscapes. Future research should evaluate this hypothesis and predictions.

Implications

Our findings give rise to two management implications. From a population perspective, we documented a low probability of detection (0.32) of calling males during peak calling. Based on this detection probability, call-count surveys would have to be repeated at least 8 times to have ≥0.95 probability of detecting the subspecies given it was present. In addition, although peak calling in our study occurred during early-mid June, past research indicates that the timing of peak calling of quails can shift in response to weather (Hansen and Guthery, 2001). Thus, we recommend that call-count surveys for chestnut-bellied scaled quail involve not only repeat surveys (≥8 replications) but also be conducted during May–August to ensure that peak calling is captured. From a habitat perspective, pricklypear was an important nesting substrate for chestnut-bellied scaled quail. Nests also were situated in areas of high brush cover and diversity. Consequently, preservation of pricklypear and stands of diverse, native brush should be a high consideration when planning brush-management practices in southern Texas. In addition, given the profound effects that root plowing can have on native-plant communities, we do not recommend root plowing as a general brush-management practice (although it may be considered in specific, unique circumstances) if preservation of chestnut-bellied scaled quail habitat is a goal.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Fidel Hernández: Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Richard H. Sinclair:** Writing – review & editing, Investigation, Data curation. **Holley N. Kline:** Writing – review & editing, Investigation, Data curation. **Eric D. Grahmann:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Timothy E. Fulbright:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **David B. Wester:** Writing – review & editing, Software, Methodology, Formal analysis. **Jeremy Baumgardt:** Writing – review & editing, Software, Methodology, Formal analysis. **Michael Hehman:** Writing – review & editing, Resources, Project administration, Methodology, Conceptualization.

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Declaration of Generative AI and AI-Assisted Technologies in the Writing Process

During the preparation of this work the author(s) did not use any Generative AI or AI-assisted technologies in the writing process.

Supplementary materials

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