

CHOICES OF FEEDING HABITAT BY RELICT MONTEZUMA QUAIL IN CENTRAL TEXAS

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ABSTRACT.—Montezuma Quail (*Cyrtonyx montezumae*) were studied at the eastern edge of their range on the Edwards Plateau, Texas. Population densities were similar on a moderately grazed and an ungrazed ranch. Feeding habitat, revealed by holes dug for wood sorrels (*Oxalis drummondii*) and the discarded sorrel hulls, was compared to concurrently unused habitat containing the sorrels but no holes and hulls. Significantly different means and reduced variation in the chosen habitat features were considered criteria of habitat selection. The quail chose feeding sites primarily on the basis of tall-grass (hiding) cover but also chose deep, dry soils on slopes in relatively open Madrean evergreen woodland. Tall-grass cover predicted the location of feeding sites most often on the grazed ranch, where that cover-type was patchier. When grazing removes 40-50% of the tall grasses in an area, we believe the quail are extirpated (a nearby, formerly occupied, overgrazed site had only 25% tall-grass cover). Received 3 Feb. 1989, accepted 9 Oct. 1989.

Montezuma Quail (*Cyrtonyx montezumae*) inhabit open, evergreen woodlands in Mexico and the Southwest, including isolated areas in central and Trans-Pecos Texas. The species was studied in southern Arizona (Wallmo 1954; Marshall 1957; Bishop and Hungerford 1965; Brown 1976, 1978, 1982) and Chihuahua, Mexico (Leopold and McCabe 1957) but is poorly known in Texas (Fuentes 1903), where it has declined in numbers and range over the past century (Oberholser 1974, Gehlbach 1981). Originally, Montezuma Quail ranged across the southern Edwards Plateau, Texas, into the Trans-Pecos, but native birds are now very local (Sorola 1986) and on one endangered species list (Texas Organization for Endangered Species 1988).

Leopold and McCabe (1957) observed that the birds declined when overgrazing destroyed their food supply, although Brown (1978, 1982) noted that heavy grazing increased food but still caused a decline in the quail, because escape or hiding cover was reduced. The removal of most available forage grasses eliminated Montezuma Quail locally in southern Arizona (Brown 1982). Major plant foods and escape cover were coextensive in Texas, so overgrazing might have destroyed both features (Gehlbach 1981).

Montezuma Quail dig the bulbs of sedges (*Cyperus*) and wood sorrels

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(*Oxalis*) in Arizona (Bishop and Hungerford 1965; Brown 1978, 1982), Chihuahua (Leopold and McCabe 1957), and Texas (pers. obs.). Upon excavating these major foods, the birds eat fleshy portions, leaving hulls in or near a small hole (Leopold and McCabe 1957, Bishop and Hungerford 1965, Brown 1978). This sign of feeding may be used for census purposes (Brown 1976), and by contrast to nearby areas without fresh holes, as an indicator of habitat choice.

Despite continued grazing, Montezuma Quail persist in the Rocksprings area of the Edwards Plateau. This is not general knowledge (cf. Johnsgard 1973, Oberholser 1974, Sorola 1986), and there is no quantitative study of the species or its environment in Texas. We observed birds and their choices of feeding habitat at two Edwards Plateau ranches, employing principles of investigation and data analysis similar to McCallum and Gehlbach (1988). We tested the null hypothesis that Montezuma Quail feed indiscriminately throughout occupied habitat and used the results of this study to appraise a formerly occupied and apparently overgrazed locale.

STUDY SITES

The ranches (17 km SW Rocksprings, Edwards County, 500 m) were a sheep-goat-cattle operation, about 10 ha/animal unit, and a deer and turkey-hunting reserve ungrazed by domestic livestock for four years. At each ranch, we located a 25-ha study site inhabited by Montezuma Quail year-round. These sites had similar populations as judged from quail flushed during habitat assessments in September 1981 through July 1982 (mean = 0.08 ± 0.05 [SD] and 0.10 ± 0.07 birds/ha, respectively, $N = 13$ each, Wilcoxon $P > 0.50$). However, we could not account for repeated observations of the same birds. Northern Bobwhites (*Colinus virginianus*) were present in similar numbers (0.18 ± 0.10 birds/ha, Wilcoxon $P = 0.43$).

A brushy, evergreen woodland of 521 stems/ha, dominated by *Quercus fusiformis*, *Diospyros texana*, *Rhus virens*, and *Sophora secundiflora*, characterized the grazed ranch. *Q. fusiformis*, *D. texana*, and *Berberis trifoliolata* dominated the more open, evergreen woodland of 140 stems/ha on the ungrazed ranch. Dominant tall grasses at both sites were *Aristida wrightii*, and *Bouteloua curtipendula*, followed by *Schizachyrium scoparium*. Short grasses were primarily *Hilaria belangeri* in the open and *Stipa leucotricha* under woody cover and grew on flats by contrast to tall grasses on the slopes. *Juniperus ashei* and *Pinus cembroides* were present on both ranches, adding to the general aspect of Madrean evergreen woodland (Amos and Gehlbach 1988).

Kickapoo Caverns State Park (50 km SW of Rocksprings, Edwards-Kinney counties, 550 m) was our third site, studied in March and September 1988. Montezuma Quail were present historically (S. Sorola, pers. comm.) but absent during the study (they were found only 1 km away). This park had been a sheep-goat-cattle ranch but was ungrazed one year before sampling. Its evergreen woodland of 312 stems/ha was dominated by *Q. fusiformis* and *D. texana*, as well as *J. ashei* and *P. cembroides*. *B. trifoliolata* and *Karwinskia humboldtiana* were the leading shrubs; *A. wrightii* and *H. belangeri* were the most important tall and short grasses, respectively.

Because Montezuma Quail habitat elsewhere is at least 500 m higher in elevation, drier,

and has a July–September rainfall pattern (monsoon) that triggers nesting (Leopold and McCabe 1957), we noted climatic and reproductive differences at the species' eastern edge of range on the Edwards Plateau. In our study, area mean annual rainfall is 54 cm, but as much falls in April–June (33%, mean temperature = 24°C) as in July–September (35%, 28°C; Larkin and Bomar 1983). We found hatchlings on June 15th, and young birds were about half-grown on September 18th, suggesting late summer nesting as well.

METHODS

On the ranches, two perpendicular 10-m line-intercept transects measured ground cover at each feeding place, indicated by a concentration of recently dug holes and associated bulb hulls of the wood sorrel (*Oxalis drummondii*) (=chosen habitat). Vegetation included seven categories: tall grass (>0.3 m), short grass (<0.3 m), oak-leaf litter, other-leaf litter, erect forbs, prostrate forbs, and dead wood (sticks, logs, bark). Physical cover was either Edwards limestone outcrops or bare soil, sometimes with a partial cover of *Selaginella* sp.

At each transect intersection, we measured the distance to and canopy diameter of the nearest tree (lowest limbs above 0.3 m) and shrub (limbs below 0.3 m) in each of the four quarters and synthesized the data per stratum (Cottam and Curtis 1956). Also measured at the intersection were slope angle, site exposure (N = 1, NE = 2, E = 3, etc.), and soil depth, plus temperature and moisture at average bulb depth (=5 cm; *O. drummondii* was not visible above ground all year, hence could not be measured directly). Each variable was a known or potential aspect of food or shelter based on the literature, a week of pre-study observations, and general experience (Gehlbach 1981).

After each feeding habitat sample was taken, concurrently unused habitat was selected randomly within 100 m and assayed in the same manner. This habitat lacked holes and hulls but had *O. drummondii*, at least in the fall when the wood sorrel was most evident. A thorough search for signs of recent feeding within 10 m of each transect assured veracity of the sample, and all feeding and unused samples were marked to avoid resampling. We emphasize that we studied choice of feeding habitat rather than habitat versus non-habitat, because Montezuma Quail were seen at or near both feeding and unused sites on both ranches.

Samples were taken monthly in March–May (spring, quail paired and calling), June–July (summer, hatchlings found), September–November (fall, half-grown birds), and December–February (winter, coveys). The data were analyzed by season as well as by site, because we anticipated changing demands by the birds and vegetational differences related to season in addition to feeding preferences related to grazing impact and landscape variation.

Analyses of variance (ANOVAs) of all 18 physical and biotic parameters, arcsine or log-transformed as necessary, tested mean differences between the ranches, seasons, and habitats. Significant ($P = 0.05$) parameters were then employed in multiple stepwise regressions (MSRs) to reveal the amount of variation in feeding versus unused habitat determined by each parameter simultaneously. Habitat choices are also shown by reduced variation in the data from used sites (Ratti et al. 1984), and degree of selectivity is indicated by the amount of variance reduction (McCallum and Gehlbach 1988). Thus, we calculated coefficients of variation (CVs) of the significant parameters and used two-tailed Wilcoxon signed-ranks tests of the CVs to evaluate the postulated differences in variation.

Only those variables that significantly described feeding habitat at both ranches in the spring and fall were measured at Kickapoo Caverns State Park. They were soil depth, oak-leaf litter, other-leaf litter, tall-grass, and shrub cover. Field methods were the same except that 30 random samples of potential feeding habitat were taken over 25 ha. Potential feeding habitat was defined from the ranch study as having tall grasses and wood sorrels. Since we

hypothesized that the park and ranch feeding habitats were the same, we compared them with ANOVAs of the five indicator variables.

RESULTS

Ranches.—The grazed and ungrazed ranches differed according to 13 of the 18 habitat parameters. For example, the grazed site had greater slope, tree density, and more bare ground (highest F -values). Of special importance, however, are variables that were the same at both ranches (exposure, soil depth and moisture, tall- and short-grass cover), because all except exposure were important distinguishing features of feeding habitat.

At the grazed ranch, feeding and unused habitats were distinct all year; 10 of the 18 parameters were significantly different. Tall- and short-grass cover (both greater in feeding habitat), tree density, soil moisture, and shrub cover (less in feeding habitat) had the highest F -values. This result was the first of six instances among 10 inter-habitat comparisons on both ranches in which tall-grass cover was a significant predictor of habitat choice (Table 1).

Feeding and unused habitats also were discernible year-round at the ungrazed ranch. Significant differences were discovered in soil depth, soil moisture, and tall-grass cover. Soil depth and tall-grass cover were greater, and soil moisture less, in the chosen feeding areas (Table 1). Among the four features involved in distinguishing habitats at both ranches, listed above, all showed smaller mean differences at the ungrazed site, suggesting more continuous habitat (less patchiness) and hence less discrimination by Montezuma Quail.

Nevertheless, the birds were selective as revealed by the smaller CVs of environmental features that significantly predicted feeding habitat (Table 1). On the ungrazed ranch year-round, CVs of all significant features averaged 40% in feeding areas compared to 58% in unused habitat (Wilcoxon $P = 0.03$). Apparently even more selectivity prevailed on the grazed ranch (\bar{x} CVs = 31% vs 50% in unused habitat, $P = 0.01$), but there was no inter-ranch difference in the reduced habitat variation associated with feeding ($P = 0.25$).

Seasons.—Significant differences among the four seasons were apparent in 10 of the 18 parameters on both ranches. The three soil features had the highest F -values. Among vegetational variables which we thought might change seasonally, both types of grass cover, other-leaf litter, and erect-forb cover increased significantly from spring into fall. Total variation explained by the MSRs was considerable in summer ($R^2 = 81\%$ grazed, 97% ungrazed) and fall ($R^2 = 72\%$ grazed, 73% ungrazed) but dropped in winter (48%, 33%) and spring (39%, 22%), possibly because

TABLE 1
 ENVIRONMENTAL FEATURES THAT PREDICT DIFFERENCES IN FEEDING HABITAT COMPARED TO HABITAT CONCURRENTLY UNUSED FOR
 FEEDING BY MONTEZUMA QUAIL^a

	Grazed ranch		<i>r</i> ² added	Unused habitat		Ungrazed ranch		<i>r</i> ² added	Unused habitat	
	Feeding habitat	Unused habitat		Feeding habitat	Unused habitat	Feeding habitat	Unused habitat			
	All-Year (N = 78 grazed, 68 ungrazed)									
Tall-grass cover (m)	13.2, 37%	6.9, 58%	0.34	Soil depth (cm)		8.3, 29%	6.4, 59%	0.18	8.3, 29%	6.4, 59%
Short-grass cover (m)	10.0, 74%	3.2, 75%	0.08	Soil moisture (%)		13.2, 35%	24.5, 56%	0.06	13.2, 35%	24.5, 56%
Tree density (N/ha)	173.0, 44%	314.0, 62%	0.03	Tall-grass cover (m)		13.0, 53%	9.3, 77%	0.05	13.0, 53%	9.3, 77%
	Spring (N = 20 grazed, 20 ungrazed)									
Soil depth (cm)	8.9, 10%	6.2, 37%	0.39	Slope (°)		3.6, 46%	1.6, 75%	0.22	3.6, 46%	1.6, 75%
	Summer (N = 14 grazed, 12 ungrazed)									
Shrub density (N/ha)	318.0, 22%	789.0, 39%	0.44	Slope (°)		2.3, 21%	5.7, 25%	0.76	2.3, 21%	5.7, 25%
Tall-grass cover (m)	16.2, 33%	10.3, 42%	0.37	Rock cover (m)		17.5, 25%	34.4, 26%	0.19	17.5, 25%	34.4, 26%
	Fall (N = 20 grazed, 14 ungrazed)									
Tall-grass cover (m)	13.3, 41%	5.6, 66%	0.43	Tall-grass cover (m)		16.8, 10%	9.2, 49%	0.02	16.8, 10%	9.2, 49%
Short-grass cover (m)	9.9, 72%	2.5, 76%	0.29							
	Winter (N = 24 grazed, 22 ungrazed)									
Tall-grass cover (m)	11.9, 29%	5.4, 67%	0.48	Soil depth (cm)		8.4, 23%	5.3, 46%	0.33	8.4, 23%	5.3, 46%

^a Features are listed in order of their explanation of significant ($P = 0.05$) variational differences between the two habitat-types on each ranch (r^2 additions to R^2 in one all-year and four seasonal multiple stepwise regressions per ranch). Means and coefficients of variation (%) are given.

unmeasured factors became more important relative to the seasonally reduced, herbaceous vegetation (Table 1).

Comparing habitats at the two ranches in spring, we found few similarities. The quail chose feeding areas with greater soil depth, more tall grasses, and fewer trees on the grazed ranch but greater slope and more dead wood, erect forbs, and shrub cover on the ungrazed ranch. Soil depth (grazed) and slope (ungrazed) were the only significant predictors (Table 1), but all indicators were significantly less variable among samples of feeding habitat on the two ranches combined. Thus, the birds were selective seasonally (\bar{x} CVs = 55% vs 97% in unused habitat, Wilcoxon $P = 0.04$).

More tall-grass cover predicted feeding habitat on both ranches in the summer, with other significant determinants being lower shrub density (grazed) and less slope and rock cover (ungrazed, Table 1). Not only was variation among the habitat factors significantly reduced in the summer feeding areas of both ranches (\bar{x} CVs = 30% vs 56% in unused habitat, Wilcoxon $P = 0.01$), it was reduced compared to feeding habitat in the spring ($P = 0.05$). This suggests even more rigorous selectivity.

By fall more tall- and short-grass cover, less soil moisture, and lower shrub density indicated feeding habitat on the grazed ranch. Less moisture and lower tree density characterized feeding areas on the ungrazed ranch, but significant predictors were the grasses and moisture (Table 1). Similarly, in winter the tall grasses indicated feeding habitat only on the grazed ranch, along with greater slope and soil depth. The latter also predicted chosen areas on the ungrazed site. Variation of both the selected and unused habitats decreased from fall to winter, although significant within-season differences remained (\bar{x} CVs = 45% vs 67% in fall and 29% vs 47% in winter, Wilcoxon $P = 0.05$).

Tall-grass cover.—This most frequently identified variable predicted feeding habitat in three seasons at the grazed ranch but only during summer at the ungrazed ranch (Table 1). By adding significant r^2 values of variables in four seasonal MSRs per ranch and comparing hierarchies of the sums of those variables in common, we found that tall-grass coverage ranked first at the grazed site and last at the ungrazed ranch (Table 2). The order of parameter influence on habitat choice was reversed ($r_s = -0.90$, $P = 0.03$). Vegetation was more important in the presence of livestock, whereas physical factors prevailed in their absence (Table 2).

State park.—The Kickapoo Caverns State Park site was quite distinct from both ranches, since four of the five indicator variables were different (Table 3). Tall-grass cover was 60% less extensive, and shrub cover 58% greater, while the leaf litter was 123–203% greater in contrast to the feeding habitat on both ranches. This suggests that the park area had been overgrazed and was unsuitable for the quail.

TABLE 2
 HEIRARCHY OF ENVIRONMENTAL FEATURES, COMMON TO BOTH RANCHES, THAT EXPLAIN
 DIFFERENCES IN FEEDING HABITAT COMPARED TO HABITAT CONCURRENTLY UNUSED FOR
 FEEDING BY MONTEZUMA QUAIL

Features (in feeding habitat)	Grazed ranch	Ungrazed ranch
Tall-grass cover (more)	1.28	0.02
Shrub density (less)	0.44	0.08
Soil depth (more)	0.39	0.34
Soil moisture (less)	0.01	0.73
Slope (more)	0.06	0.97

^a Values are the sums of significant ($P = 0.05$) r^2 additions to R^2 from four seasonal multiple stepwise regressions per ranch.

DISCUSSION

Relict Montezuma Quail persist on the Edwards Plateau, Texas. There, population densities are similar on moderately grazed and ungrazed sites ($\bar{x} = 0.09$ birds/ha). They are also similar to densities in Arizona (0.08–0.9 birds/ha; Brown 1978, 1982; Gehlbach unpubl.) and Chihuahua (0.1 birds/ha, Leopold and McCabe 1957). It appears that grass cover taller than 0.3 m is the most critical component of feeding habitat on the plateau, particularly on grazed land. Whereas tall grasses were implicated 60% of the time in our analyses of feeding sites, short grasses were involved only 20% of the time and not at all on ungrazed land (Tables 1 and 2).

As significant predictors of feeding habitat, tall grasses constituted $70 \pm 10\%$ ($\bar{x} \pm SD$) of ground cover compared to $39 \pm 11\%$ in habitat unused for feeding ($N = 6$ each from Table 1). Formerly occupied overgrazed land averaged only 25% tall grass cover, following a year of no grazing, but occupied habitat averaged 62% (Table 3). Brown (1982) found that most Montezuma Quail in southern Arizona inhabited areas having average livestock utilization levels below 46% and suggested that grazing 46–50% of the grasses produced marginal conditions. If our coverages are roughly comparable, then the chosen tall-grass habitat in central Texas is only 20–40% grazed, whereas unused habitat is marginal to unsuitable (50–72% grazed).

Our grazed and ungrazed sites had similar tall- and short-grass cover, but tall grasses were more important to Montezuma Quail on the grazed site, where they were patchier and hence scarcer. Also, the birds choose relatively open ground on the more densely wooded, grazed land. Apparently, if tall grasses are sufficient but quite patchy with respect to dense woody vegetation, a common result of grazing (Amos and Gehlbach 1988), then more grass and fewer woody plants both predict feeding habitat

TABLE 3
 POTENTIAL MONTEZUMA QUAIL FEEDING HABITAT AT KICKAPOO CAVERNS STATE PARK
 (OVERGRAZED, FORMERLY INHABITED BY THE BIRDS) COMPARED TO ACTUAL FEEDING
 HABITAT AT GRAZED AND UNGRAZED RANCHES NEARBY*

Feature	F (P)	State park (N = 30)	Ranches (N = 37)
Shrub cover (m)	8.3 (<0.001)	12.2, 51%	7.7, 47%
Tall-grass cover (m)	7.7 (<0.001)	5.0, 44%	12.4, 43%
Oak-leaf litter (m)	3.7 (=0.01)	10.3, 107%	3.4, 136%
Other-leaf litter (m)	2.6 (=0.04)	13.4, 92%	6.0, 91%
Soil depth (cm)	1.8 (NS)	6.5, 52%	8.2, 28%

* Data are means and coefficients of variation (%).

(Table 2). Perhaps there is a trade-off between the two cover-types favoring tall grasses, the more important habitat predictor, because we saw the quail take refuge in both kinds of cover but did not find feeding habitat beneath a woody canopy.

In the absence of grazing and hence presence of more continuous grass cover, tall grasses were still important year-round but particularly in summer when feeding site selection was especially rigorous. Deeper, drier soils also were critical (on the grazed land too, Table 1). We think the quail choose such soils, because we observed more wood sorrels growing in deeper soils and found their bulbs easier to dig under drier conditions. Presumably the birds are similarly constrained. Slope also emerged as a major indicator of feeding habitat on the flatter, ungrazed study site (Table 2). In spring, when rainfall is considerable, the quail choose steeper slopes that should be relatively drier because of increased runoff. But in summer they choose flatter places, since bulbs give way to insects as primary foods (Bishop and Hungerford 1965, Brown 1982), and digging apparently is not as frequent (Table 1).

The link between overgrazing and decline of Montezuma Quail has been surmised since the 1920s (Leopold and McCabe 1957) but only recently quantified (Brown 1982). We refine that link by showing reduced tall grasses and increased shrubs in potential feeding habitat at a formerly occupied locale. For the first time we demonstrate that the quail choose certain sites on the basis of hiding cover over others with presumably similar food potential. These sites have mostly tall-grasses on slopes with deep, dry soils in an evergreen woodland matrix. We suggest that both the required habitat, and thus the quail, are dispersed patchily in response to natural landscape heterogeneity and grazing impact. We postulate that grazing increases the patchiness, eventually eliminating the quail when 40–50% of the tall-grass (hiding) cover is removed.

ACKNOWLEDGMENTS

F. Speck and C. White generously allowed us to work on their ranches, and K. Bryan and D. Riskind permitted study of Kickapoo Caverns State Park before its development. B. Albers, K. Bryan, D. Chau, C. Clarke, N. Gehlbach, J. Glass, and T. Wilson assisted in the field or lab. R. Brown sent reports and suggestions. K. Gutzwiller, A. McCallum, and S. Sorola critically read the manuscript. We thank everyone.

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