



Distribution and interaction of white-tailed deer and cattle in a semi-arid grazing system

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ABSTRACT

In order to optimize production, range managers need to understand and manage the spatial distribution of free-ranging herbivores, although this task becomes increasingly difficult as ranching operations diversify to include management of wildlife for recreational hunting. White-tailed deer are sympatric with cattle throughout much of their range and are a valuable commodity in southern rangelands. The spatial distribution of deer and cattle was monitored over 1 year during four trials each lasting 12 days. In each trial six white-tailed deer (three bucks, three does) and nine cows were fitted with Global Positioning System (GPS) collars. Collars were scheduled to take a position location every 5 min to determine animal location. These data were analyzed to study animal-to-animal interactions. To minimize problems of spatial autocorrelation, data were thinned to hourly locations for assessing animal home ranges and distributions. Although there was extensive overlap in spatial distributions of deer and cattle the species exhibited strong temporal separation. The mechanism was probably a combination of avoidance of cattle by deer and different habitat requirements. Close interactions were rare, however, individual deer did not show avoidance of cattle until they were within 50 m of each other. Species distributions overlapped mainly on the most productive ecological sites such as clay loam soils and riparian areas which were favored by both species. Cattle avoided rocky terrain, so deer had almost exclusive use of rocky areas including the productive deep soil drainage areas within them. Does particularly favored these areas and the riparian areas while bucks favored the more open clay loam sites. In this shrub-dominated system both deer and cattle were often located close to ranch roads, and cattle especially used roads as paths of least resistance. Cattle were closely associated with water sources, but deer did not stay long near water or at supplemental feeding sites. Concerns that cattle will displace deer into marginal habitats, or that deer will over utilize vegetation near water and feeders, were not supported.

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1. Introduction

Land use patterns and foraging behavior of wild and domestic herbivores can have long lasting effects on plant community structure and ecosystem function (Hobbs, 1996; Turner et al., 1997), as evidenced by the worldwide problem of shrub encroachment in rangelands. Thus, understanding and managing the distribution of free-ranging herbivores is a major issue facing rangeland managers (Bailey et al., 1996). In many areas the economic value of wildlife on rangeland is becoming increasingly

significant (IAFWA, 2002), and revenue from hunting leases often provides a substantial form of additive income to traditional cattle ranching operations (Adams et al., 2000). This has resulted in a changing paradigm of rangeland management, with rangelands increasingly being managed for multispecies production, and in some instances with wildlife production as the primary goal. Successful diversification of ranching operations to include recreational use of wildlife requires further understanding species distributions and interactions. For example, managers of hunting ranches often remove all cattle based on perceived competition between cattle and deer. Yet under light grazing pressure cattle can be a useful tool in creating and maintaining habitat for deer by removing the overburden of dry grass stalks allowing light to reach the soil and stimulate the growth of more nutritious forbs and new grass (Willms et al., 1981; Jenks et al., 1996). Hence, total removal of cattle from deer hunting ranches may not be the most

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appropriate management strategy. Identifying key areas of interspecific spatial overlap and non-overlapping areas may allow more accurate multispecies management and greater revenue from the land.

In a synthesis paper on large herbivore grazing distribution patterns, Bailey et al. (1996) considered abiotic factors to be the primary determinants of large scale distribution patterns of herbivores, however, many of the studies of multispecies habitat utilization have been conducted in mountainous areas where terrain and slope have large impacts on animal distribution (Loft et al., 1993; Yeo et al., 1993; Stewart et al., 2002). In relatively flat rangeland, Owens et al. (1991) identified ranch infrastructure, such as roads, fences and water sources, as the dominant abiotic factors influencing cattle distribution, while forage abundance and brush cover were the main biotic factors.

In multispecies management, interspecific interactions may influence habitat use if sympatric species compete for space or food resources. Cattle have been shown to displace elk (*Cervus elaphus*) from meadows and other open habitats, but they have less effect on the distribution of browsers such as mule deer (*O. hemionus*) inhabiting the same area (Wallace and Krausman, 1987). Although cattle and mule deer overlap in distribution within pastures, they are usually temporally separated due to avoidance behavior by the deer (Loft et al., 1993), cattle seem to be indifferent to the presence of deer and are not aggressive towards them (Krämer, 1973; Loft et al., 1993). White-tailed deer are reputedly less tolerant of cattle than are mule deer (Krämer, 1973). Density of cattle also has an effect on spatial interactions, for example in Texas white-tailed deer were seen to share the range with cattle in a continuous grazing system but avoided concentrations of cattle in short duration grazing rotations (Cohen et al., 1989).

Despite this body of knowledge, little is known about the interaction between deer and cattle in shrub-dominated rangelands and how these interactions affect spatial distribution of ungulates in large pastures. The goal of this study was to examine the distribution and interaction of cattle and white-tailed bucks and does in relation to ecological sites, and anthropogenic features such as roads, water sources and localized food resources (high protein supplements provided for deer in free-choice feeders). Use of GPS (Global Positioning System) collars eliminated any confounding effects of human presence altering animal distributions. Our hypotheses were: (i) cattle and white-tailed deer would be temporally separated by deer avoiding close contact with cattle; (ii) cattle and deer would be spatially separated by ecological site due to different dietary requirements, although spatial overlap would be most likely on the more productive sites; and (iii) distributions of deer and cattle would be different with respect to anthropogenic features, cattle should stay close to roads and water sources while deer, as a hunted species, should have limited contact with features frequented by humans.

2. Methods

2.1. Site description

The study was conducted on a 6764 ha ranch, in Uvalde County, Texas (29°15'0.02"N, 100°5'54.01"W) located in the transition zone between the Edwards Plateau and South Texas Plains ecological regions. Vegetation and management practices on the ranch were typical of much shrub-dominated rangeland. Most of the topography of the ranch consisted of gently undulating caliche ridges with thin calcareous soils of low productivity (Stevens and Richmond, 1970), the terrain became increasingly stony towards the northeastern corner of the ranch. Typical vegetation consisted

of mixed thorn shrub community containing guajillo (*Acacia berlandieri*), blackbrush (*Acacia rigidula*), and cenizo (*Leucophyllum frutescens*) shrubs, interspersed with prickly pear cactus (*Opuntia lindheimeri*). Grass cover was sparse but included red grama (*Bouteloua trifida*) and Wright's threeawn (*Aristida purpurea*). Low lying areas of the ranch contained deeper clay loam soils. These more fertile, relatively flat, areas supported scattered honey mesquite (*Prosopis glandulosa*) trees and a mixed shrub community which included whitebrush (*Aloysia gratissima*) and Texas persimmon (*Diospyros texana*). Trees, such as honey mesquite and live oak (*Quercus virginiana*), were associated with deeper soils and drainages. Grasses included common curly-mesquite (*Hilaria belangeri*), buffalo grass (*Buchloe dactyloides*) and Texas winter-grass (*Stipa leucotricha*). In all areas diverse forb cover varied with rainfall pattern and abundance.

The climate was semi-arid and precipitation patterns were erratic. Mean annual rainfall was approximately 620 mm, but during this study annual precipitation measured on the ranch was above average (883 mm) in 2004 then declined to far below average (180 mm) in 2006. Average annual maximum and minimum temperatures were 35.5 °C and 13.7 °C, respectively.

Within the ranch, this study focused on a 2091 ha pasture delineated by an ephemeral river and steep terrain on the southern side and by high fencing on the other three sides, thus restricting animal dispersal. After the first trial a low fence, excluding cattle from the riverbed and adjacent riparian areas was completed, this restricted cattle but not deer to a 1211 ha pasture. The river was not a barrier to deer movements, for most of the year the only surface water was in two semi-permanent pools and most of the water flowed subsurface through the limestone cobbles. Cattle stocking rate within the pasture was 1 cow-calf unit to 35 ha. Deer density was approximately 1 animal per 6 ha. Within the 1211 ha pasture cattle and deer had access to water at three sites, deer had access to an additional three sites across the cattle fence. Supplemental feed in the form of soybeans was provided year round for the deer at six free-choice feeders, cattle were fenced out of these feeders. Once a week the cattle received a supplement of 20% protein range cubes (Livengood Feeds, Lockhart, TX) fed on the road where ever they were located. Since there was no set feeding location, and usually no feed left after the cattle departed, this practice was unlikely to affect deer distribution. In the last trial frequency of supplementation of cattle was increase to twice a week due to drought induced decline in forage quantity and quality. In hunting season (November through January) a little shelled corn was fed at dawn and dusk at 12 additional sites and scattered on the roads to increase visibility of the deer.

2.2. Experimental design

Spatial distribution of deer and cattle was monitored during four trials each lasting 12 days. Trial 1 ran from 23 July to 3 August 2005, this was in summer of a high rainfall year with ample forage available for the animals; trial 2 ran from 5 to 16 November 2005 in late fall when food availability was declining, this trial was during deer hunting season; trial 3 ran from 8 to 19 March 2006 and was scheduled for spring green up although vegetative production was limited by lack of spring rains; trial 4 ran from 15 to 26 July 2006 in summer during drought conditions when little high quality natural forage was available.

Six adult deer were fitted with GPS collars (Lotek GPS 3300S with drop-off latch, Lotek Wireless, Inc., Newmarket, Ontario, Canada) and nine adult cross-bred Angus cows were also collared (Lotek GPS 3300LR). Due to possible gender specific differences in habitat requirements (Kie and Bowyer, 1999; DePerno et al., 2003) and hunting pressure, we considered bucks and does separately.

Differences in distribution between bucks and does in the first trial, August 2006, were biased due to poor capture distribution of deer, all does were captured near the river and all bucks near the northern fence. Better distribution of deer was achieved in the subsequent trials when one buck and one doe were captured by helicopter drop-net in each of the eastern, central and western sections of the pasture to limit effects of capture site on deer distribution relative to ecological sites. Each deer was fitted with a GPS collar and an ear-tag to ensure that these individuals were not recaptured in subsequent trials. It is estimated that there were approximately 200 white-tailed deer in the cattle pasture. Despite the use of a small number of collars in each trial, the experimental design allowed us to sample a total of 24 deer (12%) throughout the experiment, thus meeting the minimum statistical sampling requirements (Yamane, 1967). Cows were selected randomly for collaring but with the stipulation that no animal was collared twice during the study. Collars were programmed to synchronously take 1 location every 5 min. Data was differentially corrected to improve position accuracy to ≤ 5 m (Lotek, 2005). Location of roads, water, and feeders were plotted with a submeter accuracy GPS unit (R. Cooper using a Trimble GeoXT, Sunnyvale, CA).

2.3. Deer–cattle interactions

Collar data from each animal was imported into a GIS database (Arcview, ESRI, Redlands, CA) and the coordinate pairs (X, Y) were calculated for all locations within a percent dilution of position (PDOP) < 6 . Data from all animals were synchronized at 5 min intervals to detect incidents of close contact. However, because location data collected every 5 min is correlated, it violates statistical independence. Preliminary analysis (Perotto and Cooper unpublished data) indicates that 1 h intervals between locations can significantly reduce correlation and therefore data were thinned to 1 h intervals by including only one randomly selected location per hour for statistical analysis. Euclidean distance between each deer and cow (bucks and cows, does and cows separately) was calculated and distances summarized to estimate the mean and standard error for all occurrences for every hour within the trial period.

Small scale analysis was conducted using tracking analyst to quantify the number of instances within the entire dataset when a collared deer and cow came within 100 m of each other. The closest distance between the two animals was measured and the movement response of the deer to the cow was recorded as avoidance or non-avoidance. Due to the rarity of close interspecific contact events information was combined for all trials.

2.4. Habitat use

Soils database was acquired from the Soil Survey Geographic database (SSURGO) to generate a layer of rangeland ecological sites (NRCS, 2007). Hourly data from cows and deer was summarized by ecological sites (Table 1), and the proportion of occurrence within each ecological site calculated for bucks, does, and cows. A Chi-square test was performed based on the proportion of each site in the study area (expected data) and the percentage of occurrence of individuals within sites (observed data). Ecological sites were classified as favored or avoided if proportional use by the animals was significantly higher or lower ($P < 0.05$) than availability in the study area.

2.5. Distance to anthropogenic features

Location of cattle and deer relative to water sources, deer feeders, and roads was examined using Arcview, cattle feeding sites were not included as cattle were only fed once a week and not

Table 1

Characteristics of ecological sites (from United States Department of Agriculture Soil Conservation Service Soil Survey of Uvalde County, Texas): slope, soil depth, potential productivity in dry years and texture of terrain

Ecological site	Slope	Soil depth	Productivity	Terrain
Loamy bottomland	Level	Variable	High	Flat
Clay loam	Level	Deep	High	Flat
Shallow Rio Grande Plains	Undulating	Deep	Low	Flat
Deep upland	Level	Deep	High	Stony
Igneous hill	Variable	Deep	Low	Stony
Shallow ridge	Undulating	Shallow	Low	Stony
Low stony hill	Undulating	Shallow	High	Stony
Shallow Edwards Plateau	Level	Shallow	High	Rocky
Stony ridge	Undulating	Shallow	Low	Rocky

at any fixed time or location. A distance surface (1 m resolution) was generated from each feature in the study area and the Euclidean distance values were obtained for each animal location within the surface grid. Cumulative frequencies were plotted to give an overview of animal distributions relative to anthropogenic features. To assess animal distributions when they are most likely to be active (Montgomery, 1963; Coulombe et al., 2006; Meek, 2007), location data within 2 h before sunrise and 2 h after sunset, were examined, again using a 1 h time interval between consecutive locations to minimize spatial autocorrelation. Mean and standard error was calculated for cow, buck and doe distances from anthropogenic features. An equal number of random points were generated and distance values obtained for all features. Actual animal locations and random points were compared using analysis of variance ($\alpha = 0.05$) to test if animals were distributed randomly relative to anthropogenic features.

3. Results

3.1. Interactions between deer and cattle

There was very little close interaction between the collared white-tailed deer and cattle. Within the 12 km² pasture collared individuals of the two species consistently stayed about 2 km apart at any point in time (Table 2). Slight variations in distance occurred during the daily cycle but the magnitude was only about 300 m which is minimal compared to the overall distance between the species. Bucks came slightly closer to cattle at night in July 2006 than in previous trials, but these differences were not significant. Gender had no effect on the distribution of deer relative to cattle.

Deer and cattle occasionally came in close contact with each other but such events were extremely rare, over all four trials collared cattle and deer only came within 100 m of each other on 121 occasions (e.g. 1 contact in about 628 deer location fixes). Moving deer generally passed cattle at 53 ± 2 m distance, but were twice recorded as close as 10 m. There was no evidence that the deer changed course to avoid cattle. In one instance, a buck and a cow were stationary, presumably resting, within 70 m of each other. On 30 occasions cattle approached a stationary deer. Responses of these deer were variable but in general distances at which deer tended to

Table 2

Mean (\pm S.E.) distance (m) between individual deer and cattle, data taken at 5 min intervals, thinned to hourly data and averaged over 12 days

Trial	Buck to cow		Doe to cow	
	Mean	S.E.	Mean	S.E.
August	2510	33	2154	26
November	2182	25	2352	41
March	2341	18	1984	29
July	1896	85	1826	21

move away or stay when a cow passed by were significantly different ($t_{28} = 2.113, P < 0.05$), deer tended to be displaced by cattle approaching within 46 ± 5 m ($n = 15$), but tolerated cattle at 64 ± 7 m ($n = 15$) distance.

3.2. Use of ecological sites

The distribution of cattle on the different ecological sites was disproportional to their availability in the habitat in all trials ($\chi^2_{7-9} = 43.24-94.95, P < 0.001$) (Fig. 1). In the first trial, when cattle had access to the riverbed and adjacent riparian areas, 64% of cattle relocations were in riparian loamy bottomland sites and 22% were in clay loam sites, thus cattle favored loamy bottomland ecological sites, and used clay loam sites in similar proportion to availability. Use of stony or rocky terrain was correspondingly low. In subsequent trials, the aforementioned construction of a cattle fence to protect the riparian areas restricted cattle access to the

loamy bottomlands. During the three subsequent trials, $68 \pm 5\%$ of cattle relocations were recorded in clay loam ecological sites, and use of remaining areas of loamy bottomland was proportional to availability. Use of shallow ridge sites by cattle increased once the fence was completed, but cattle still avoided the rougher terrain, only $19 \pm 4\%$ of relocations were in rocky areas even though such terrain constituted half (50%) of the study area. The deep upland sites within these rocky areas were not utilized by cattle.

Over the entire year, white-tailed deer used ecological sites in similar proportion to their availability within the pasture ($\chi^2_9 = 6.25, P > 0.05$), and they made equal use of rocky areas ($37 \pm 6\%$), riparian areas ($30 \pm 6\%$) and clay loam sites ($31 \pm 3\%$). However, deer did exhibit seasonal selectivity in use of ecological sites ($\chi^2_2 = 25.84-66.75, P < 0.05$), deer tended to favor the more productive riparian, clay loam and deep upland sites.

In August 2005 bucks were distributed away from the riverbed and adjacent loamy bottomlands. They used the shallow ridge and

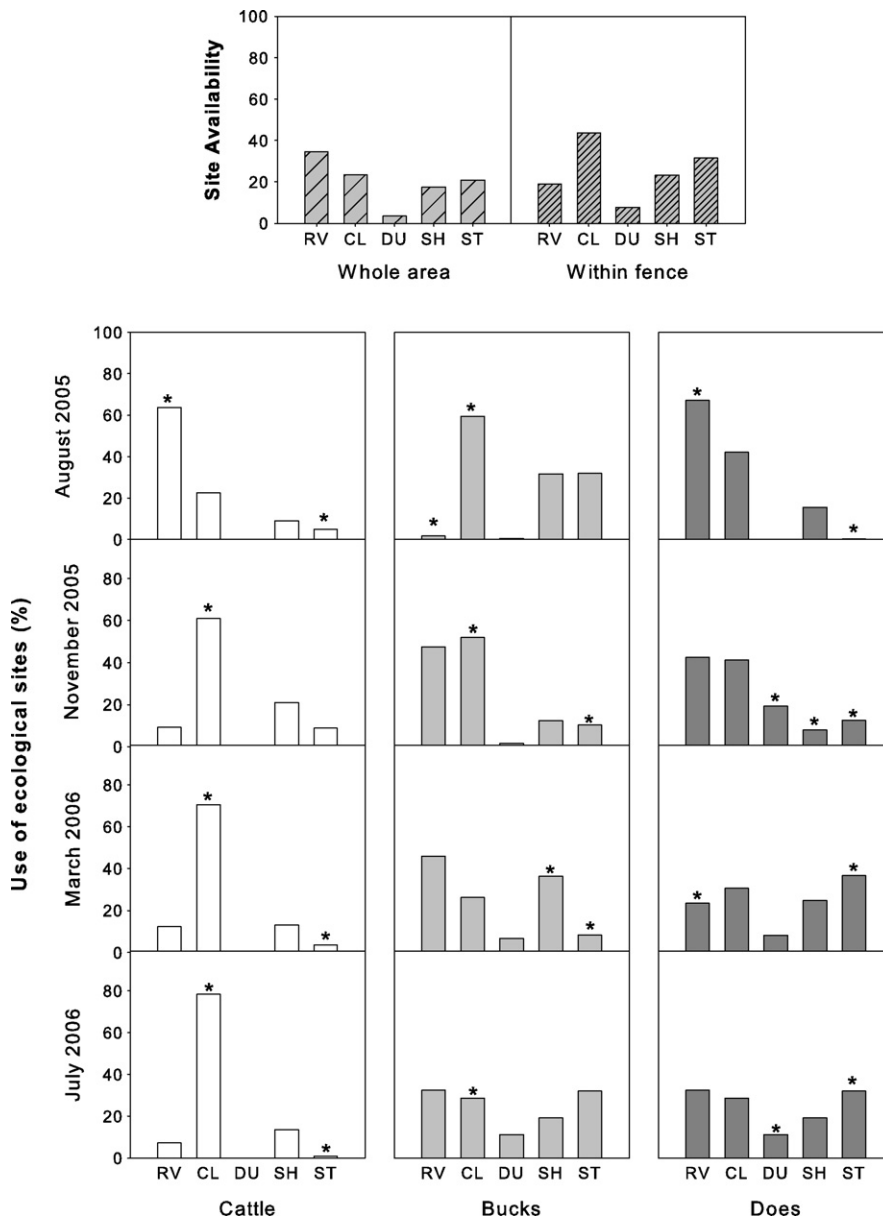


Fig. 1. Ecological site availability (a) and seasonal ecological site use (b) by cattle and white-tailed deer. RV: riverbed and loamy bottomland, CL: clay loam and shallow Rio Grande Plains, DU deep upland and igneous hill, SH: shallow ridge, ST: low stony hill, shallow Edwards Plateau and stony ridge. (*) denotes a difference ($P < 0.05$) in use and availability of an ecological site.

stony ridge sites in proportion to availability and favored the clay loam areas. In November bucks continued to favor clay loam sites, but use of shallow ridge and stony ridge sites had decreased and use of riverine areas increased. In March 2006 bucks used clay loam sites in proportion to availability and favored shallow ridge sites, but selected against the more stony areas. In July bucks again favored clay loam sites.

In August 2005 does favored loamy bottomlands near the riverbed, used clay loam sites in accordance with their availability, and under-utilized stony ridge sites. Then in November they used riparian areas and clay loam sites in proportion to availability and favored deep upland sites, but not the adjacent stony or rocky areas. Does continued to use clay loam sites according to availability in March, and favored stony ridge sites. Although often relocated in the riverbed, they under-utilized adjacent loamy bottomlands. In July does favored the deep upland sites and the adjacent low stony hill sites.

3.3. Animal distance from anthropogenic features

The ranch had an extensive network of dirt roads (37 m of road/ha), and all the animals were usually within 400 m of a ranch road (Fig. 2). Bucks retained a fairly constant distribution relative to roads. Compared to the bucks, cattle and does tended to be further from roads in August, but closer to roads in November and March, in July all animal distributions relative to roads were similar. Frequently animals were very close to the roads. Overall, two-thirds (64 ± 3%) of cattle relocations were within 100 m of a road and

Table 3

Seasonal distribution (% relocations) of cattle and white-tailed deer on ranch roads and within 100 m of roads, water sources and deer feeders

Animal	Trial	On road	Road	Water	Feeders
Cattle	August	18.61	53.05	5.02	1.95
	November	12.93	61.80	4.07	0.89
	March	17.08	77.77	8.80	2.26
	July	19.22	64.01	9.70	1.62
Bucks	August	3.69	55.93	0.83	2.20
	November	6.56	41.66	0.34	0.60
	March	2.79	40.25	1.25	1.30
	July	4.44	54.54	1.65	1.99
Does	August	2.14	39.51	1.22	3.54
	November	6.05	59.50	0.11	0.06
	March	0.55	61.48	0.55	0.00
	July	1.51	55.58	1.51	0.55

17 ± 3% were within 10 m of the centerline, i.e. probably on the road (Table 3). Cattle proximity to roads increased slightly from August through March. Half the relocations of deer (53 ± 8%) were also within 100 m of a road and 5 ± 2% were within 10 m of a road. In November and March bucks were relocated within 100 m of roads less frequently than does, yet November was the time when deer were most frequently relocated on the roads.

Animals were rarely >1.5 km from water. Cattle were consistently distributed closer to water sources than were deer, and could be found within 100 m of water for 5% of relocations in August and November, increasing to 9% of locations in March and

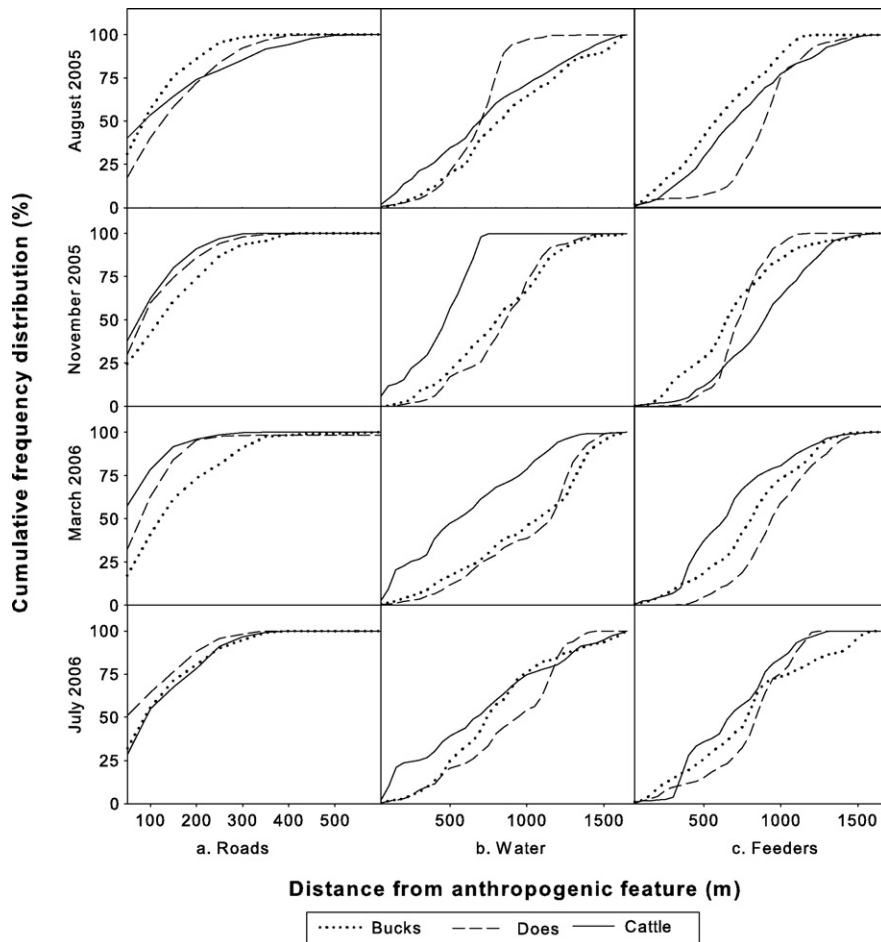


Fig. 2. Seasonal cumulative distance distribution of cattle and white-tailed deer from anthropogenic features on the ranch. Cattle solid line, bucks dotted line, does dashed line.

July. Deer spent little time close to water sources, and were only recorded within 100 m of water on $1 \pm 0.6\%$ of relocations. The distribution of bucks and does relative to water sources was similar.

Cattle could not access the food in the deer feeders, so these feeders had little attraction for them, yet in March and July cattle were often slightly closer to the feeders than the deer were. Cattle were only within 100 m of a deer feeder on $2 \pm 1\%$ of relocations. Placement of deer feeders ensured that deer were rarely >1.5 km from a source of supplemental feed. Bucks were consistently distributed closer to the feeders than does were. However, deer were rarely found very close to the feeders, only $1 \pm 1\%$ of relocations placed deer within 100 m of a feeder.

3.4. Animal distance from anthropogenic features during active periods

During the 2 h before and after sunrise each day, when animals are likely to be active and foraging, all animals remained distributed closer to roads than expected from random placement ($P < 0.001$), and there were significant differences between seasons (Fig. 3). Cattle stayed closest to roads in March, and were farthest away in the summer months of August and July. They were slightly nearer to roads in the evening as opposed to morning. Deer also tended to be nearest to roads in the evening. Bucks were closest to roads in August and July and in November. Does were closest to roads in November and March.

Averaged over the year, the distribution of cattle relative to water was not different than random, but there were strong seasonal differences ($P < 0.001$). In March the cattle were much

closer to water than random at both sunrise and sunset, but in the other trials cattle were slightly farther away from water than random distribution. Bucks and does were generally distributed closer than random to water ($P < 0.001$) particularly in the evening. The times they were farthest from water were mornings in March and July.

Cattle could not access the feed in deer feeders, so distribution of cattle is probably not influenced by placement of deer feeders, however, cattle tended to be closer than random to feeders in August and March and farther away in November and July. Bucks were generally distributed closer than random to feeders ($P < 0.001$), at all times except in March and mornings in July. In contrast, the overall distribution of does relative to feeders was no different from random, does generally stayed far from feeders, and only came closer than random to feeders in mornings in November and evenings in July.

4. Discussion

Spatial overlap between cattle and white-tailed deer was extensive, particularly in the more productive ecological sites, which are often favored by herbivores (McNaughton, 1985), however, the two species exhibited strong temporal separation. Cattle showed strong selection for the riparian areas which provided forage, shade trees for thermal balance and easy access to water. After their access to riparian areas was restricted, cattle consistently favored the clay loam areas. Although the terrain was relatively flat and slopes were gentle, cattle still avoided sloping, rocky terrain as they do in much steeper, mountainous areas (Cook, 1966; Stewart et al., 2002). The only rough terrain used frequently

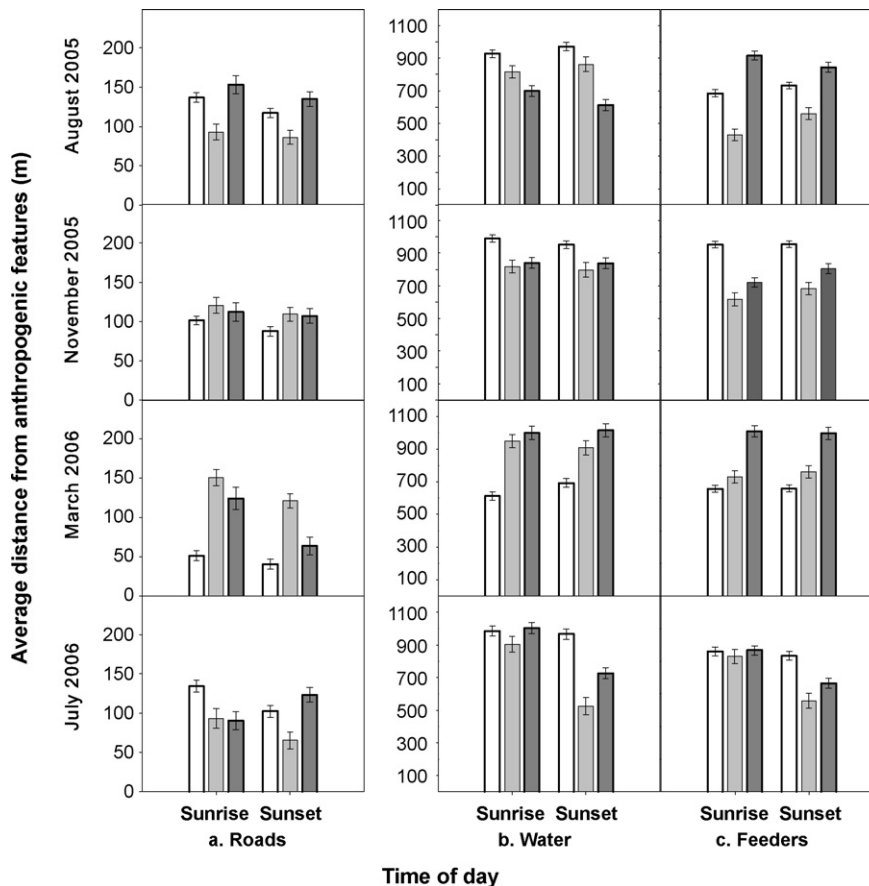


Fig. 3. Seasonal average distance with standard errors of cattle and white-tailed deer from anthropogenic features 2 h before sunrise and 2 h after sunset. Cattle white, bucks light grey, does dark grey.

by cattle was the shallow ridge ecological site which intersected the favored clay loam areas. Cattle may also have avoided the rockier areas because of the dense thorny shrub cover on these sites which provided a physical and visual barrier to foraging (Cook, 1966; Owens et al., 1991).

Deer made greater use of rough terrain, but like cattle, they favored the more productive areas, bucks tended to favor clay loam areas, while does favored riparian and drainage areas with more tree cover. These gender differences in ecological site selection are supported by observation by Kie and Bowyer (1999) in Texas, who noted that at moderate population density bucks selected the more open mesquite grasslands which are analogous to our clay loam ecological sites, whereas does with young made greater use of shrub-dominated habitat with denser cover. In a similar hot, semi-arid, region in Mexico, Bello et al. (2001) found that white-tailed does selected areas with more cover than the bucks, especially in drought conditions such as those experienced in this study. Due to cattle avoidance of rocky areas, deer had almost exclusive use of the deep upland ecological sites which consist of deep soil drainage sites within rocky terrain, these productive sites supported live oak woodland and were favored by does particularly in November and July possibly because they provide both good nutrition and thick cover for thermal regulation and for protection of fawns (Ockenfels and Bissonnette, 1984; Bowyer et al., 1998; Bello et al., 2001).

Even though there was spatial overlap in use of the more productive habitats, deer and cattle were separated temporally. Collared deer stayed approximately 2 km from cattle in all seasons with minor daily variation in distance. This distance may be overestimated due to small sample size in each trial, but it is consistent throughout the whole experiment. Thus, it is indicative of consistent temporal separation of the species. Comparable temporal separation has been reported where mule deer and cattle share foraging areas (Loft et al., 1993; Stewart et al., 2002). The rarity of close contact events between deer and cattle also supports the idea of temporal separation of species. Deer generally did not approach cattle closer than 50 m and tended to move away if the cattle came any closer. These distances are similar to former reports on interactions between mule deer and cattle which suggest 47 m (Krämer, 1973) to 75 m (Loft et al., 1993) as the minimum distances at which mule deer will tolerate cattle. White-tailed deer are considered to be less accepting of cattle than are mule deer (Krämer, 1973), but in this study cattle avoidance distances of white-tailed deer were similar to those reported for mule deer. Possibly in earlier studies disturbance by people monitoring the animals increased measurements of deer distances from cattle, but in this study use of GPS collars eliminated any confounding effects of human disturbance.

The three main anthropogenic features on this relatively flat landscape were roads, water sources and deer feeders. Animal distributions are influenced by the distribution of resources on the landscape (Roath and Krueger, 1982; Owens et al., 1991), and by the complex interaction between these features: roads lead to water and feeders, the placement of which depends on characteristics of terrain, road networks and former management decisions based on animal distributions and earlier efforts to maximize pasture utilization by attracting livestock to areas of low use.

The study ranch was typical of the region, in that the thorny shrubland was traversed by a large network of dirt roads to facilitate both cattle management and to deliver hunters to numerous hunting blinds. Two-thirds of the cattle relocations were within 100 m of roads and 17% of relocations placed them within 10 m of the road, which given the ± 5 m location error of the collars (Lotek, 2005) suggests that these cattle were likely to be traveling along the roads. Cattle are known to use roads as pathways of least

effort (Roath and Krueger, 1982; Ganskopp et al., 2000), and considering the density and thorniness of shrubs in the study area it was not surprising that animals used roads as travel corridors. Cattle were closest to roads in March and farthest away in the summer months. Owens et al. (1991) noted that cattle use of areas near roads declined as the year progressed and forage availability close to roads decreased, however, in this study there was very little green up of vegetation in spring due to drought conditions.

Deer were relocated on roads less frequently than cattle, although half their locations were within 100 m of a road. It is to be expected that the more wary deer would spend less time on the open roads. Bucks retained a constant distribution relative to roads throughout the year, but during the hunting season which began in November, does approached closer to roads, possibly drawn by the corn trailed on the roads to attract deer for census and viewing. Both cattle and deer tended to be closer to roads in the evening than in the morning. Presumably the animals use roads as routes of least effort to traverse from daytime resting areas to better foraging areas. Animals may also have been visiting supplemental feeders and water sites both of which are situated along roads.

Water is a critical resource for herbivores, particularly in the summer and during drought, as occurred in the March and July trials. Cattle were consistently distributed closer to water than deer were and the herd could often be found resting by water. In South Texas, taller trees used by cattle for thermal cover are often associated with water sources (Depew, 2005). At dawn and dusk, except in March, cattle were distributed away from water, presumably they drank during the day and moved away from water to feed. Forage depletion often occurs close to water (Roath and Krueger, 1982; Andrew, 1988), even though in March green up of herbaceous vegetation was limited it may have been enough to enable cattle to feed closer to their resting and watering sites. The cattle stayed closer to water as the year progressed and effects of the drought became more severe. In this environment Owens et al. (1991) also found that cattle are more likely to stay close to water at times when forage availability is low. Deer spent very little time at the water, but were closer to water during the active period, particularly at dusk when they probably came to drink. In an adjacent pasture on the same ranch, Depew (2005) also found that deer tend to be distributed away from water sources, although rainfall was more abundant during his study. The timing of visits to water by deer may be associated with avoidance of cattle which tend to congregate around water sources during the daytime.

Provision of supplemental feed for deer in free-choice feeders fenced off from cattle is a common management practice on south Texas ranches, although deer with access to supplemental feed still browse extensively on natural forages (Murden and Risenhoover, 1993; Doenier et al., 1997). Cattle could not access the deer feed, yet at times they were closer to feeders than the deer were, probably because feeders tend to be placed in areas accessible by vehicle and easily fenced, such as on the clay loam areas favored by cattle, rather than on rocky slopes. Bucks were consistently located closer to feeders than does. During the active periods bucks were usually closer than random to feeders except in March, when they may have been feeding on the limited spring green up of the browse plants. Does stayed far from feeders and only came close in mornings during November and evenings in July. This pattern suggests that does mainly use feeders in times of nutritional stress such as winter or drought, but do not stay near the feeders. Personal observation indicates that does and yearling bucks will often be the first animals at deer feeders in the evening, but are displaced by mature bucks as darkness falls. Therefore provision of supplemental feed may have more influence on the distribution of bucks than does.

5. Conclusion

Concerns that livestock force wildlife species to use marginal habitat were unfounded, animals shared use of the rangeland although they were separated temporally. Deer were often located in rocky areas which were little used by cattle, but they also were able to use the most productive ecological sites in greater proportion than their availability in the habitat, despite concentrated use of these areas by cattle. Deer also had almost exclusive use of the productive deep soil drainage sites occurring within the rocky areas. Although the slopes were gentle, the rocky substrate and dense thorn scrub deterred cattle from accessing these areas which were particularly favored by does. Management implications of this distribution of livestock and wildlife are that rough terrain can be managed primarily for deer and other wildlife, while flat areas with deeper soils require mixed species management. Anthropogenic features also influenced animal distribution. Cattle, and to a lesser extent deer, made heavy use of roads and grazing pressure can be expected to be greatest near roads. Cattle tended to congregate near water, but deer just made brief visits to resources such as water and supplemental feed. Cattle are known to overgraze vegetation around water sources, but the distribution of deer away from water and feeders allays concerns that deer may also deplete forage resources around water and feeders (Cooper et al., 2006). Since deer seem to avoid close contact with cattle, they and other wildlife, may gain more benefit from water sources and feeders placed in rocky areas where cattle are less likely to congregate, than when these resources are placed in the areas shared with cattle. By locating species-specific management in appropriate areas both cattle and wildlife production can be maximized.

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References

- Adams, C.E., Wilkins, N., Cooke, J.L., 2000. A place to hunt: organizational changes in recreational hunting, using Texas as a case study. *Wildl. Soc. B* 28, 788–796.
- Andrew, M.H., 1988. Grazing impact in relation to livestock watering points. *Trends Ecol. Evol.* 3, 336–339.
- Bailey, D.W., Gross, J.E., Laca, E.A., Rittenhouse, L.J., Coughenour, M.B., Swift, D.M., Sims, P.L., 1996. Mechanisms that result in large herbivore grazing distribution patterns. *J. Range Manage.* 49, 386–400.
- Bello, J., Gallina, S., Equihua, M., 2001. Characterization and habitat preferences by white-tailed deer in Mexico. *J. Range Manage.* 54, 537–545.
- Bowyer, R.T., Kie, J.G., van Ballenberg, V., 1998. Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? *J. Mammal.* 79, 415–425.
- Cohen, W.E., Drawe, D.L., Bryant, F.C., Bradley, L.C., 1989. Observations on white-tailed deer and habitat response to livestock grazing in South Texas. *J. Range Manage.* 42, 361–365.
- Cook, C., 1966. Factors affecting utilization of mountain slopes by cattle. *J. Range Manage.* 19, 200–204.
- Cooper, S.M., Owens, M.K., Cooper, R.M., Ginnett, T.F., 2006. Effect of supplemental feeding on spatial distribution and browse utilization by white-tailed deer in semi-arid rangeland. *J. Arid Environ.* 66, 716–726.
- Coulombe, M.L., Masse, A., Cote, S.D., 2006. Quantification and accuracy of activity data measured with VHF and GPS telemetry. *Wildl. Soc. B* 34, 81–92.
- DePerno, C.S., Jenks, J.A., Griffin, S.L., 2003. Multidimensional cover characteristics: is variation in habitat selection related to white-tailed deer sexual segregation? *J. Mammal.* 84, 1316–1329.
- Depew, J.J., 2005. Habitat selection and movement patterns of cattle and white-tailed deer in a temperate savanna. MS Thesis, Texas A&M University, College Station, Texas, USA.
- Doerner, P.B., DelGiudice, G.D., Riggs, M.R., 1997. Effects of winter supplemental feeding on browse consumption by white-tailed deer. *Wildl. Soc. B* 25, 235–243.
- Ganskopp, D., Cruz, R., Johnson, D.E., 2000. Least-effort pathways? A GIS analysis of livestock trails in rugged terrain. *Appl. Anim. Behav. Sci.* 68, 179–190.
- Hobbs, N.T., 1996. Modification of ecosystems by ungulates. *J. Wildl. Manage.* 60, 695–713.
- International Association of Fish and Wildlife Agencies, 2002. Economic Importance of Hunting in America. IAFWA, Washington, DC.
- Jenks, J.A., Leslie, D.M., Lochmiller, R.L., Melchior, A.M., McCollum, F.T., 1996. Competition in sympatric white-tailed deer and cattle populations in southern pine forests of Oklahoma and Arkansas. *Acta Theriol.* 41, 287–306.
- Kie, J.G., Bowyer, R.T., 1999. Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection, and dietary niche. *J. Mammal.* 80, 1004–1020.
- Krämer, A., 1973. Interspecific behavior and dispersion of two sympatric deer species. *J. Wildl. Manage.* 37, 288–300.
- Loft, E.R., Kie, J.G., Menke, J.W., 1993. Grazing in the Sierra Nevada: home range and space use patterns of mule deer as influenced by cattle. *Calif. Fish Game* 79, 145–166.
- Lotek, 2005. Lotek Wireless, Inc. <http://www.lotek.com/gps3300.htm> (accessed July 2005).
- McNaughton, S.J., 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecol. Monogr.* 55, 259–294.
- Meek, M.G., 2007. Spatio-temporal distribution of white-tailed deer (*Odocoileus virginianus*) relative to prescribed burns on rangeland in South Texas. MS Thesis. Texas A&M University, College Station, Texas.
- Montgomery, G.G., 1963. Nocturnal movements and activity rhythms of white-tailed deer. *J. Wildl. Manage.* 27, 422–439.
- Murden, S.B., Risenhoover, K.L., 1993. Effects of habitat enrichment on patterns of diet selection. *Ecol. Appl.* 3, 497–505.
- NRCS, 2007. <http://www.esis.sc.egov.usda.gov/> (accessed in June 2007).
- Ockenfels, R.A., Bissonnette, J.A., 1984. Temperature related responses in north-central Oklahoma white-tailed deer. In: Krausman, P.R., Smith, N.S. (Eds.), *Deer in the Southwest: A Workshop*. Arizona Cooperative Wildlife Research Unit and School of Renewable Natural Resources. University of Arizona, Tucson, AZ, pp. 64–67.
- Owens, M.K., Launchbaugh, K.L., Holloway, J.W., 1991. Pasture characteristics affecting spatial distribution of utilization by cattle in mixed brush communities. *J. Range Manage.* 44, 118–123.
- Roath, L.R., Krueger, W.C., 1982. Cattle grazing and behavior on a forested range. *J. Range Manage.* 35, 332–338.
- Stevens, J.W., Richmond, D.L., 1970. Soil survey of Uvalde County, Texas, U.S. Department of Agriculture, Natural Resources Conservation Service, Washington, DC, USA.
- Stewart, K.M., Bowyer, R.T., Kie, J.G., Cimon, N.J., Johnson, B.K., 2002. Temporospatial distributions of elk, mule deer and cattle: resource partitioning and competitive displacement. *J. Mammal.* 83, 229–244.
- Turner, M.G., Pearson, S.M., Romme, W.H., Wallace, L.L., 1997. Landscape heterogeneity and ungulate dynamics: what spatial scales are important? In: Bissonette, J.A. (Ed.), *Wildlife and Landscape Ecology: Effects of Pattern and Scale*. Springer-Verlag, New York, pp. 331–348.
- Wallace, M.C., Krausman, P.R., 1987. Elk, mule deer, and cattle habitats in Central Arizona. *J. Range Manage.* 40, 80–83.
- Willms, W.A., Bailey, A.W., McLean, A., Tucker, R., 1981. The effects of fall defoliation on the utilization of bluebunch wheatgrass and its influence on the distribution of deer in the spring. *J. Range Manage.* 34, 16–18.
- Yamane, T., 1967. *Statistics: An Introductory Analysis*, 2nd ed. Harper and Row, New York, p. 886.
- Yeo, J.J., Peek, J.M., Wittinger, W.T., Kvale, C.T., 1993. Influence of rest-rotation cattle grazing on mule deer and elk habitat use in east-central Idaho. *J. Range Manage.* 46, 245–250.