

SOCIAL BEHAVIOR AND MOVEMENT ECOLOGY OF NILGAI ANTELOPE

A Thesis

by

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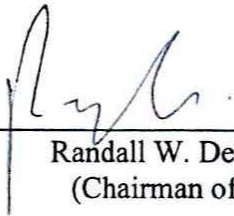
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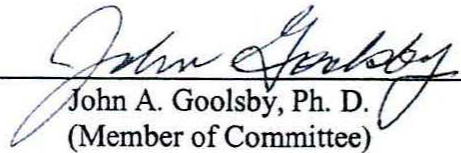
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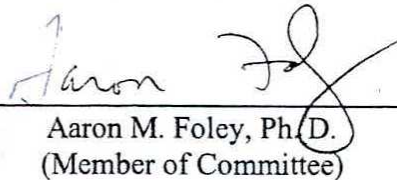
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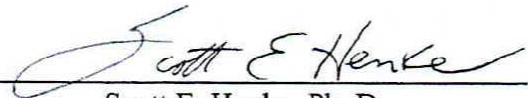
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ABSTRACT

Social Behavior and Movement Ecology of Nilgai Antelope

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Nilgai antelope (*Boselaphus tragocamelus*) are an exotic ungulate species in Texas. Native to India, Nepal, and Pakistan, nilgai have expanded into much of coastal southern Texas and northeastern Mexico since their introduction in 1924–1949. The presence of nilgai in Mexico and South Texas has complicated the eradication of cattle fever ticks (CFT; *Rhipicephalus annulatus* and *R. microplus*). Cattle fever ticks can transmit bovine babesiosis to cattle, a serious economic threat to the U.S. cattle industry. With CFT quarantine areas established in South Texas, ranches with infested cattle must comply with extensive eradication requirements. Wildlife can hinder eradication efforts because white-tailed deer (*Odocoileus virginianus*) and nilgai are alternative hosts for CFT. Control methods, such as acaricide-treated baits, are available for deer. Nilgai do not respond to bait, which is a major challenge for controlling the spread of CFT. One unique aspect of nilgai ecology is their use of latrines, or repeated defecation at a localized site. In addition, nilgai are not impeded by standard livestock fencing, and often push under fences at well-established crossing sites. The existence of these repeatedly visited areas present an opportunity for CFT treatment through application of acaricides using remotely

activated sprayers. With limited information on nilgai ecology, there is pressure to understand nilgai latrine and fence crossing behavior to design efficient CFT treatment measures. I analyzed the density, size, activity, and placement of nilgai latrines. I used trail cameras to assess frequency, time of day, sex, and age of nilgai that used latrines and all animals that used fence crossings. Also, I used genetic markers to determine how many individual nilgai use latrines. Knowledge of nilgai movement and behavior will help identify areas to target with remotely activated acaricide sprayers. The results of this study will have important implications for the development of treatment methods for eradication of CFT in the U.S.

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CHAPTER I

BACKGROUND AND LITERATURE REVIEW

Background

Nilgai antelope (*Boselaphus tragocamelus*) are native to most of India, Nepal (Dinerstein 1980), and Pakistan (Mirza and Khan 1975). Nilgai are monotypic in the *Boselaphus* genus, included in the bovidae family bovinæ subfamily, within the Boselaphini tribe. Nilgai were introduced to South Texas in 1924–1949 (Leslie 2008). Free-ranging populations have become established and now extend from northeastern Mexico to much of coastal South Texas. Overall, there is limited information about the ecology and behavior of nilgai. Besides a few recent studies on nilgai movement and diet in South Texas (Moczygemba et al. 2012, Hines 2016, Foley et al. 2017), and nilgai crop depredation in India (Bayani and Watve. 2016), research on nilgai social behavior is limited to a few observational studies done during the 1970s to 90s (Sheffield et al. 1971, Fall 1972, Mirza and Khan 1975, Sheffield 1983, Singh 1995).

Ecology

Nilgai often form sexually segregated groups for most of the year (Fall 1972, Singh 1995), but group size varies among seasons (Singh 1995). Males are often solitary, especially during December–March (Fall 1972, Singh 1995), or occur in small groups of 2–9 individuals (Singh 1995). In India, females were often observed in large groups of 10–17 individuals during December–March, and mean group size was smallest ($\bar{x} = 4$) during April–November (Singh 1995). The change in group size for males and females could be attributed to the calving season, which peaks during June–August in India (Singh 1995). Breeding may occur throughout the year (Sheffield et al. 1971, Fall 1972, Singh 1995), with the highest peaks in breeding during December–early March or September–March in South Texas (Fall 1972, Sheffield et al. 1983).

Dinerstein (1980) noted a peak in breeding around January in India. Nilgai often give birth to twins (Fall 1972, Sheffield et al. 1983, Bagchi et al. 2008) and may have triplets (Fall 1972, Sheffield et al. 1983). Gestation lasts 243–247 days (Brown 1936, Sheffield et al. 1983), and calves weigh about 6.8 kg at birth (Hediger 1955, Fall 1972). Nilgai are strongly sexually dimorphic. Mature males have horns, grey pelage, and are physically larger (\bar{x} body mass = 241 kg, $n = 39$) vs. cows (\bar{x} body mass = 169 kg, $n = 23$; Sheffield et al. 1983). It is typical for antelopes to have large differences in body size and mass between the sexes since males continue to develop after females, and have prolonged growth depending on rank in the male hierarchy (Jarman 1974).

Many populations of antelope have a female-biased adult sex ratio (Jarman 1974, O’Kane and Macdonald 2016, Debata 2017). From 2,147 nilgai observed in Haryana, India, the mean adult sex ratio was 1 male:1.09 females in December 1989–November 1991 (Singh 1995). In forested areas in Maharashtra, India, Bayani and Watve (2016) found 1 male:4.95 females ($n = 273$) during monsoon seasons, and 1 male:0.58 females during post-monsoon ($n = 572$). A Texas study found 1 male:0.92 females from 3,206 nilgai observed during July 1968–April 1969 (Fall 1972). From 2014–2019, sex ratios were recorded during aerial surveys of 2 South Texas ranches and found 1 male:1.44–2.98 females, and 1 male:1.57–2.56 females (East Foundation, unpublished data).

Tigers (*Panthera tigris tigris*) and dholes (*Cuon alpinus*) are known to predate on adult nilgai in their native range (Hayward et al. 2014, Basak et al. 2018); golden jackals (*Canis aureus*) are known to predate on nilgai calves (Prerna et al. 2015). However, adult nilgai in Texas have no natural predators besides humans, or an occasional transient mountain lion (*Puma concolor*; East Foundation, unpublished data). Bobcats (*Lynx rufus*) and coyotes (*Canis*

latrans) predate on white-tailed deer fawns (Cook et al. 1971), but it is not known if these species cause significant mortality to nilgai calves.

The most detailed study of nilgai movement ecology to date involved 30 nilgai fitted with satellite GPS collars in South Texas (Foley et al. 2017). The median annual home range size for males was 4,665 ha (range = 571–20,809) and 1,606 ha (range = 848–29,909) for females (Foley et al. 2017). An earlier study in South Texas found no difference in mean home range sizes between males and females, with means over 8,000 ha (Moczygemba et al. 2012). Some nilgai bulls maintain small home ranges (Qureshi 1991, Foley et al. 2017). Qureshi (1991) suggested dominant bulls had smaller home ranges compared to lower ranking bulls. These studies (Moczygemba et al. 2012, Foley et al. 2017) found nilgai home ranges to be much larger than native white-tailed deer (427–922 ha for male deer; Hellickson et al. 2008), and highly variable among individuals. These large home ranges indicate the potential for nilgai to expand into new areas rapidly (Moczygemba et al. 2012, Foley et al. 2017).

Nilgai densities are influenced by water availability in their native range in India and Nepal (Bagchi et al. 2008), and water may exert a similar influence in subtropical South Texas where droughts frequently occur. In India, Singh (1995) observed peak feeding time at about 1600–1700 hr during a non-monsoon winter season. Singh et al. (2017) found nilgai activity patterns peaked during early mornings and late evenings in South Texas during August–October 2016 ($n = 114$).

Nilgai are intermediate feeders (Sheffield 1983, Singh 1995, Hines 2016), with the ability to switch among forage classes from browse to grasses (Hines 2016). During drought conditions, when forage is limiting, nilgai diets shift towards the browse-intermediate continuum, versus during non-drought conditions nilgai shift towards an intermediate-grass diet (Hines 2016). One

study from India found that nilgai diets consisted of 72-91% grass and 9-28% browse (Singh 1995). Analysis of nilgai rumen contents in Texas revealed diets of 60% grasses, 25% forbs, and 15% browse (Sheffield 1983). Feeding observations in India showed Doob or Bermuda grass (*Cynodon dactylon*) contributed the highest proportion of nilgai diet (31-53%). Other commonly consumed plants include *Salvadora oleoides*, *Prosopis cineraria*, *Capparis sepiaria*, *Prosopis juliflora*, and *Acacia nilotica* (Singh 1995). In Texas, Sheffield (1983) found that nilgai consumed *Paspalum* spp., *Setaria* spp., *Cenchrus* spp., *Eragrostis* spp., *Eleocharis* spp., *Cyperus* spp., *Cassia fasciculata*, *Rhynchosia* spp., *Sida spinose*; honey mesquite (*Prosopis glandulosa*), live oak (*Quercus virginiana*), Berlander's wolfberry (*Lycium berlandieri*), and desert hackberry (*Celtis pallida*). Of note, pods of *Prosopis* spp. are commonly consumed in both India and Texas (Sheffield 1983, Singh 1995). One major management issue in India is nilgai crop raiding (Khan 2014). This problem has escalated in recent years because of the lack of suitable habitat (Khan 2014). Khan (2014) predicted this loss in habitat led to an increase in food competition in forested areas with other wildlife. Crop raiding has led farmers to implement scaring tactics on nilgai, with use of colored ribbons, firearms, fire, fences (electric, wire, and wooden), "scare-crows," and sound (Khan 2014). While nilgai crop raiding is not a major issue in South Texas, nilgai may compete with both livestock and native wildlife for forage.

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CHAPTER II

LATRINE ECOLOGY OF NILGAI ANTELOPE

ABSTRACT Nilgai antelope (*Boselaphus tragocamelus*) are native to most of India, Nepal, and Pakistan, and were introduced to Texas rangelands during the 1920s – 1940s. Nilgai have expanded into much of coastal South Texas and northern Mexico. Little research has been done on nilgai ecology in either their native or introduced ranges. One poorly understood aspect of nilgai ecology is their use of latrines, or repeated defecation at a localized site. While latrines are common on unpaved ranch roads, there has never been a formal study on nilgai latrine use. From April 2018–March 2019, I studied nilgai latrines at 3 sites in South Texas. My objectives were to 1) determine density, area, and placement of latrines, 2) determine seasonal frequency, sex, and age classes of nilgai that use latrines, 3) determine individual nilgai use of latrines via DNA analysis, and 4) assess the social function of latrines for nilgai. I found latrines to be abundant with no apparent selection to specific vegetation communities, and dynamic in persistence and visitation rates. Nilgai latrine densities were greater than population densities, indicating nilgai must use multiple latrines; latrines were visited every 2–3 days on average. Camera traps and fecal DNA results revealed latrines were mainly (70%) visited and defecated on (89% for DNA samples, 92% in photos) by bulls; visitations often (75%) occurred during evening–night (1700–0459 hr). The greatest frequency of visits and number of latrines occurred during the peak in the nilgai breeding season during December–February. Photographs and genetic analysis of feces indicate repeated visits from the same individuals. Cows occasionally used latrines and sometimes were followed by bulls showing flehmen responses after the nilgai cow defecated or urinated on the latrine. Based on occurrences of flehmen responses, mating, and fighting, I conclude latrines are used by dominant bulls for territory demarcation, and display of social

dominance to both cows in estrus and subordinate bulls. Cows likely use latrines to communicate reproductive status. This study is the first assessment of the importance of latrines for nilgai social communication. Results provide basic ecological information on nilgai movements and behaviors, which will help managers better create management plans for this species in their introduced and native ranges.

KEYWORDS behavior, *Boselaphus tragocamelus*, dung piles, Indian antelope, latrines, nilgai antelope, olfactory communication, social structure

Nilgai antelope (*Boselaphus tragocamelus*) are native to most of India, Nepal (Dinerstein 1980), and Pakistan (Mirza and Khan 1975). Nilgai were introduced to South Texas during 1924–1949 (Leslie 2008), and free-ranging nilgai populations now extend from northeast Mexico to much of coastal South Texas. Nilgai are abundant in South Texas, with estimates of over 36,700 animals (Traweck and Welch 1992). Nilgai provide a significant economic benefit as a valued game animal. Understanding of nilgai social behavior is based on observational studies done in the 1970s to 90s (Sheffield et al. 1971, Fall 1972, Mirza and Khan 1975, Sheffield 1983, Singh 1995), recent studies on nilgai movement and diet in South Texas (Moczygemba et al. 2012, Hines 2016, Foley et al. 2017), and nilgai crop depredation in India (Bayani and Watve 2016). One poorly understood aspect of nilgai behavior is their use of latrines, where individuals repeatedly defecate on a localized site. Latrines are commonly referred to as communal dung piles, dung heaps, or middens.

The use of defecation and urination for scent-marking creates species- and individual-specific pheromones, and is a common form of communication among mammals (Ralls 1971, Wyatt 2003). Proposed drivers for scent-marking for the use of communication include kin

recognition (Ramsay and Giller 1996), communication of reproductive status (Walls et al. 1989, Palanza et al. 1994), maintenance of social hierarchies (Gosling and Wright 1994, Gosling et al. 1996), intra-sexual information exchange (Wronski et al. 2013), and to mark home range or territories (Gorman 1984, Clapperton et al. 1988, Gosling 1990, Simons et al. 1994, Lenti Boero 1995). Many animals use latrines for chemical communication (Brown and MacDonald 1985), including species of antelope, gazelle, rhinoceros, monkeys, and mesocarnivores, such as the European badger (*Meles meles*; Kruuk 1978).

Placement of latrines may depend on the intended function; some species place latrines in the center of their home range, such as the dik-dik (*Madoqua* spp.; Hendrichs and Hendrichs 1971) and klipspringer (*Oreotragus oreotragus*; Dunbar and Dunbar 1974). Scent-marking in the center of a home range could be for social group communication (Dröscher and Kappeler 2014, Jordan et al. 2007). Other species place latrines to mark territory boundaries, including the European badger (Kruuk 1978), and oribi (*Ourebia ourebi*; Brashares and Arcese 1999).

Placement of scent marks for territorial demarcation occurs in areas with high probability of detection by conspecifics (Gosling 1981, Gosling and Roberts 2001), such as boundaries or trails (Gosling 1981, 1982). If territories are too large for an animal to visit boundaries regularly, scent marking focus should be near the center of the territory (Gosling and Roberts 2001). Animal group size also may influence the placement of scent marks (Mills and Gorman 1987). For instance, large clans of spotted hyenas (*Crocuta crocuta*) with small home ranges marked territorial boundaries, whereas hyenas in small clans with large territories marked the center of the territory because of a limited time budget (Mills and Gorman 1987). Abundance of markings may not be related to territory size (Brashares and Arcese 1999), but could relate to location of home-range cores (Wronski and Plath 2010).

Physical location of defecation within a latrine may convey meaning to conspecifics. For instance, territorial white rhinoceros (*Ceratotherium simum*) defecate in the center of the latrine, whereas subordinates defecate on the outer edge (Marneweck et al. 2018). In the case of dik-dik, males scrape female feces and overmark as a means of mate-guarding to show monogamous pairing (Hendrichs 1975, Brotherton 1994, Brotherton et al. 1997). This makes female defecations hard to distinguish, but evidence of scraping may indicate use by a female (Brotherton 1994, Brotherton and Manser 1997).

The use of latrines can vary by sex, as male Grant's gazelle (*Nanger granti*; Estes 1991), Thomson's gazelle (*Eudorcas thomsonii*; Walther 1978), kongoni (*Alcelaphus buselaphus*; Gosling 1974), oribi (Brashares and Arcese 1999), and vicuña (*Vicugna vicugna*; Vilá 1994) mostly defecate on latrines. In fact, territory marking by males is common amongst mammals, and is primarily a function of intrasexual competition (Gosling and Roberts 2001). Marking territories could serve as a display of territory ownership, presence, rank, and ability to fend off intruders (Gosling 1982, Sillero-Zubiri and McDonald 1998, Gosling and Roberts 2001). Females also may display a territorial social function for latrine use, and may defend territories along with a mate or against conspecifics (Jarman 1974, Hendrichs 1975, Dunbar and Dunbar 1980). Females may use latrines to advertise reproductive receptivity to males (Blüm 1985, Rodgers et al. 2015), or show home range ownership, as with sifaka (*Propithecus verreauxi*) female groups (Lewis 2005).

Rates of scent marking and latrine defecations can vary depending on the function and social dynamics of the animal. If latrine function serves for territorial demarcation in males, one would predict that scent marks are placed on boundaries more frequently (Dröscher and Kappeler 2014), and males would scent-mark more often than females (Wronski et al. 2006).

The number of neighboring males, or an intruder defecation also could increase the rate of scent marking (Brashares and Arcese 1999, Black-Decima and Santana 2011). Rates of defecation may increase with breeding seasons if latrines advertise female receptivity (Dunbar and Dunbar 1974, Novellie et al. 1984, Kranz 1991, Roberts and Dunbar 2000, Jordan et al. 2007). The size of latrines could relate to use; large latrines may be from long-term use or use by large numbers of animals (Walther 1984, Gosling 1985).

Typically, latrines are for intraspecies communication, but there are accounts of interspecies use of latrines (Sharma et al. 2009). In India, nilgai occasionally defecate on the same latrines as chinkara (*Gazella bennettii*) and four-horned antelope (*Tetracerus quadricornis*; Sharma et al. 2009). It is unknown to what function demarcation of other species latrines serve, whether it is for interspecies communication, maybe mistaking the latrine as a conspecific intruder, or simple defecation prompted by olfactory cues. The four-horned antelope is the closest relative to nilgai, and use latrines for communication between sex and age classes (Sharma et al. 2009). Nilgai defecate on nilgai offal, near screwworm lure (a synthetic compound that mimics rotting flesh), and animal carcasses (Sheffield et al. 1983, Goolsby et al. 2017); these have strong odors suggesting an olfactory prompted defecation. In one study in India, nilgai latrines appeared more exclusive to forested areas and were not detected in agricultural fields, suggesting differences in latrine placement related to foraging grounds (Bayani and Watve 2016).

Basic ecological information is lacking for nilgai antelope. There has never been a formal study on nilgai latrines, so the function of latrine use in nilgai is unknown. Latrine use is an important aspect of their biology, that with further understanding will help uncover valuable knowledge on nilgai movements and social behaviors. My objectives were to:

- 1) determine density, area, and placement of latrines
- 2) determine seasonal frequency, sex, and age classes of nilgai that use latrines
- 3) determine individual nilgai use of latrines via DNA analysis
- 4) combine insights from objectives 1–3 to assess the social function of latrines for nilgai

STUDY AREA

This study took place on 3 sites in South Texas, the East Foundation's East El Sauz and Santa Rosa Ranches, and the Russell Ranch. The East Foundation is an Agricultural Research Organization that manages over 87,000 ha of rangeland across South Texas to promote the advancement of land stewardship through ranching, science, and education. East Foundation properties are maintained as native rangeland and working cattle ranches.

The East Foundation's East El Sauz Ranch is 10,984 ha which borders the community of Port Mansfield, Texas, in Willacy County (26°40'N, 97°35'W). Port Mansfield had annual average precipitation of 64.3 cm and average mean temperature of 23.2°C (1998–2018; Prism 2018). The El Sauz Ranch is located in the Coastal Sand Plains, Lower Rio Grande Valley, and Laguna Madre Coastal Marshes ecoregions (Bailey et al. 1994). The Coastal Sand Plains contains active sand dunes, closed-depression ponds, and mid- to tall-grass prairie. The Lower Rio Grande Valley ecoregion is dense and diverse grassland, shrubland, and low woodland communities, with mostly Quaternary clay-loams and sandy clay-loam soils. The Laguna Madre Coastal Marshes are known for a hypersaline lagoon system, seagrass meadows, and tidal mud flats (Bailey et al. 1994). The characteristics from all 3 of these ecoregions are observed at El Sauz. Common vegetation communities include live oak (*Quercus virginiana*) woodlands, mesquite (*Prosopis glandulosa*) woodlands, gulf cordgrass (*Spartina spartinae*) grasslands,

seacoast bluestem (*Schizachyrium scoparium*) grassland, and marshhay cordgrass (*Spartina patens*) grassland.

The East Foundation's Santa Rosa Ranch is 9,000 ha located near the community of Riviera, Texas, in Kenedy County (27°13'N, 97°51'W). Riviera had annual average precipitation of 70.7 cm and average mean temperature of 22.8°C (1998–2018; Prism 2018). The Santa Rosa Ranch is located in the Coastal Sand Plain ecoregion (Bailey et al. 1994). Soils include the Palobia loamy fine sand, Falfurrias-Cayo complex, Sarita, Nueces, and Sauz fine sand, and Yturria fine sandy loam (WSS 2018). Dominant vegetation communities include mesquite woodlands, huisache (*Acacia farnesiana*) woodlands, live oak woodlands, and spiny aster (*Leucosyris spinosa*) wetlands.

The Russell Ranch is 289 ha near the community Rio Hondo, Cameron County, Texas (26°12'N, 97°26'W). Rio Hondo had average annual precipitation of 68 cm, and an average mean temperature of 23.8°C (1998–2018; Prism 2018). Dominant vegetation includes honey mesquite thornscrub, Guinea grass (*Urochloa maxima*), and prickly pear cacti (*Opuntia engelmannii*). The Russell Ranch is located in the Lower Rio Grande Alluvial Floodplain ecoregion (Bailey et al. 1994). This ecoregion includes alluvial sands and clay, with mostly Vertisols and Mollisol soils (WSS 2018). The Lower Rio Grande Alluvial Floodplain ecoregion is the most subtropical ecoregion of Texas (Bailey et al. 1994).

The East Foundation conducts annual aerial surveys for nilgai on each of their properties. These surveys involve flying transects via helicopter and using distance sampling (Thomas et al. 2002) to estimate population size. During 2017, aerial helicopter surveys indicated about 1 nilgai per 11 and 12 ha, on El Sauz and Santa Rosa respectively (East Foundation, unpublished data).

No population estimates are available for the Russell due to the small size and closed canopy; however, nilgai sightings and sign were abundant (L. Zoromski, personal observation).

METHODS

I defined a latrine as a group of ≥ 5 fecal deposits within a 1 m² area. Latrines are often distinctive, where repeated defecation results in a large, oval-shaped mound. Individual pellet groups are typically difficult to distinguish within latrines unless freshly deposited (<1 week). I categorized latrines by freshness based on the freshest feces on a latrine. Fresh latrines were used recently (<2 weeks), with feces dark brown to black in color. Intermediate latrines were light brown (>2 weeks), but the timing of the most recent defecation may be difficult to determine. Feces in old latrines were weathered (~40 days), with a white and tan coloration, indicating the latrine was not used for many weeks. Appearance of freshness is highly variable since it is dependent on environmental conditions. For example, if it rained within a few hours before freshness classification, the latrines may be damp and appear darker than a latrine subject to hotter or drier weather.

Density, area, and placement of latrines

I drove a utility vehicle on all unpaved ranch roads on the 3 sites to survey for latrines. Ranch roads were made of crushed caliche stone or sand 2-track. Surveys occurred during Fall 2017, 2018, and Spring 2018, 2019, with a total of 131 km driven. Fall surveys were October–November, except the Russell Fall 2018 survey was conducted in January because the ranch was inaccessible due to flooding. Spring surveys were late April–early June. I recorded area (max. length and perpendicular width), max. height above ground, GPS location, and usage (fresh, intermediate, or old feces) on every latrine observed. Single fecal groups that did not form latrines were initially recorded in Fall 2017, but not in the subsequent surveys because single

piles were so abundant. I digitized roads (scale 1:1,000) and latrine locations using ArcGIS ArcMap 10.5.1 (ESRI©, Redlands, CA) to determine average distance between latrines, and location relative to road intersections and vegetation communities. I used an average road width of 5 m for each site to estimate density of on-road latrines, assuming all latrines in roads were detected. I used an East Foundation vegetation classification shape file (East Foundation, unpublished data) to classify latrines into vegetation community classes. There was no quantitative vegetation classification for Russell. However, most of the site is thick mesquite thornscrub and grassland pastures, so I categorized Russell latrines into general thornscrub and grassland classes. If a road divided 2 vegetation communities, the road was classified as “Transitional.”

To estimate density of off-road latrines, I assigned stratified random generated linear transect groups (North-South orientation) in major vegetation communities using ArcGIS. I walked these transects, or drove a UTV when able, to record latrine area, GPS location, and usage. I did not assign transects to all vegetation communities since these surveys were time-consuming and I wanted simply to estimate general ranch-level densities; thus community-specific densities were not needed. At El Sauz, I assigned a group of 10 transects, 50 m apart, and 500 m in length in each of the 5 major vegetation communities: live oak woodlands, mesquite woodlands, gulf cordgrass grasslands, seacoast bluestem grasslands, and marshhay cordgrass grasslands (Fig. 2.1). For Santa Rosa, I assigned groups of 10 transects, 50 m apart, and 500 m in length for each of the 4 major vegetation communities: live oak woodland, mesquite woodland, spiny aster wetland, and huisache woodland (Fig. 2.2). At Russell, I randomly assigned 4 groups of 6 transects, 200 m in length, spaced 50 m apart, stratified to have 2 within grasslands and 2 within mesquite thornscrub communities (Fig. 2.3). Transects were

shorter for Russell than East Foundation Ranches due to the smaller property size. I used distance sampling (Thomas et al. 2002) to estimate abundance of off-road latrines on each site. For each latrine encountered, I recorded the perpendicular distance from the transect to each latrine. Single nilgai fecal piles that did not form latrines were recorded, but not used in the estimation of latrine abundance. Assumptions of distance sampling were satisfied for off-road latrine surveys since latrines were stationary, latrines were not recounted (GPS locations were taken), exact distance measurements were taken, and all latrines on the transect line were detected (Thomas et al. 2002). I estimated density of off-road latrines using distance sampling analysis in the R software package Distance (R Core Team 2013, Miller 2017).

Seasonal frequency, sex, and age classes of nilgai that use latrines

I randomly selected 10 latrines at El Sauz, 10 at Santa Rosa, and 4 at Russell from latrines identified through the on-road surveys to monitor with camera traps (Reconyx© HyperFire HC500 or XR6 UltraFire, Reconyx, Holmen, WI; Moultrie© A-5 Gen2 MCG-12688 Moultrie feeders, Alabaster, AL). Half of the cameras were placed on randomly selected large latrines ($>6 \text{ m}^2$) and half on latrines $<6 \text{ m}^2$ at each ranch, under the expectation that larger latrines receive more visitations than small latrines. Camera heights (range 39–125 cm) and distance from latrines (range 210–536 cm) were variable, and dependent on the location and area of the latrine. I programmed the cameras to take a 3-photograph burst with a 10 s delay (Moultrie) or 15 s delay (Reconyx), with high detector sensitivity. I deployed cameras from April 2018–March 2019, and classified the first 2 weeks of successful photos per month (336 hours per month). Every 2 weeks, I checked cameras to replace memory cards, measure latrines, and assess freshness of fecal deposits on latrines (fresh, intermediate, or old). If a latrine was classified as “old” for more than 4 weeks, the camera was moved to a new latrine. All animals captured in the

photographs were recorded as “on,” “near,” or “away” from the latrines. Animals “on” the latrine either had a foot on the latrine, or their head over the latrine. Animals “near” latrines were either between the camera and the latrine or around the latrine, and acknowledged the latrine via sniffing or walking towards it. Animals “away” were either far off in the background in photographs, or did not appear to acknowledge the latrine (i.e., browsing a nearby tree). Both animals near and on latrines were included in analyses as “visits.” I also recorded whether animals “defecated” (displayed posture to defecate or urinate), sniffed, or displayed other behavioral responses (i.e., flehmen, mating, fight) at latrines.

I cataloged photographs using Reconyx© Mapview Professional™ Software. Nilgai were classified into age classes: old adult (bulls only), adult, subadult, and calf, similar to Singh (1995). There is no precise method for determining age of wild nilgai, so I based these categories on physical attributes. Nilgai bull pelage changes as they age, from brown pelage when young, to a steel gray-black as they mature. For bulls, “old adult” refers to steel gray in color, fully developed horns, barrel-shaped chest, with a thick neck and body. Many old adult bulls have scars from previous fights. “Adult bull” is similar to “old adult”, but less physically robust, and relatively smaller barrel chest. “Subadult” males have full grown horns, and are beginning to develop steel gray pelage, but still have brown hair. Male calves are sometimes hard to distinguish from females if the horns have not yet developed, but were recorded when visible. Male and female calves were classified together in the “calf” category for analysis. It is difficult to categorize female nilgai into multiple adult age classes, unlike for males. I categorized females as calf, subadult, and adult. Females are without horns and brown in color, with some having interspersed light gray fur. Subadult females have a relatively thin head and body compared to adult females.

To understand time of day when nilgai visited or defecated on latrines, I categorized time data into 8 parts of the day. Each category was 3 hours, starting with 0500–0759 hr since 0500 hr best encompassed the time dawn or the first hour of light began during this study.

Individual nilgai use of latrines

The process of DNA extraction, Polymerase Chain Reaction (PCR), and DNA analysis provides a method to identify individual nilgai. I obtained nilgai tissue samples as a source of high-quality DNA, and extracted DNA from samples using a commercial (DNeasy® Blood and Tissue Kit), with protocols recommended by the manufacturer (Qiagen Inc., Hilden, Germany). I evaluated DNA microsatellite loci that have amplified in other species of bovids and cervids (Anderson et al. 2002, DeYoung et al. 2003). I screened 20 markers, including BL25, BM203, BM415, BM4208, BM6438, BM6506, BM848, BovPRL, Cervid 1, D, ETH152, INRA, ILSTS, K, N, O, OarFCB193, OCAM, P, and Q (Anderson et al. 2002). I included a sexing marker (S4B) to determine if feces were deposited by males or females; the X- and Y-chromosome specific alleles of the amelogenin gene can be detected using small fragment sizes, and are a good candidate for non-invasive samples (Kageyama et al. 2004, Rivière-Dobigny et al. 2009). I amplified selected loci individually, pooled the resulting PCR products, and loaded onto an ABI 3130xl DNA sequencer (Applied Biosystems, Foster City, CA) for separation and detection of alleles. I quantified fragment sizes and allele bins using the software GeneMapper 4.0 (Applied Biosystems). I estimated probability of identity using the computer program Cervus 3.0 (Kalinowski et al. 2007) to ensure that the markers had sufficient resolution to identify individuals. After successfully genotyping nilgai through high-quality DNA, I evaluated the markers for use on fecal DNA in a mark-recapture study on latrine ecology.

I collected fresh fecal samples from the 24 camera-monitored latrines every 7–8 days for 5 weeks (9 January 2019 through 9 February 2019), at El Sauz, Santa Rosa, and Russell. I classified fecal samples by “freshness” (1 = wet coating, very soft, light brown, 2 = wet coating, soft, dark brown, 3 = dry coating, hard, dark brown). I took photographs of each visit to ensure collection of only new samples each week. Each latrine was monitored with a trail camera for an independent assessment of usage and to gauge time since deposition of fecal samples. To reduce potential for contamination, I handled the samples with latex gloves and changed gloves in between each sample. I collected a top pellet from fresh groups, from only newly distinguishable piles, using the weekly photographs for reference. Fecal samples were placed in 2-mL screw-top tubes containing DETs (DMSO/EDTA/Tris/salt) buffer (Frantzen et al. 1998). The buffer includes 20% dimethyl sulfoxide, 0.25M sodium-EDTA, 100 mM Tris, pH 7.5, and NaCl to saturation (Seutin et al. 1991). Samples were stored in a shaded container with an ice pack in the vehicle and transported to a -20°C freezer within 10 hours of the time of collection and kept at that temperature until extraction. I extracted DNA from fecal samples using the QIAamp® DNA Stool Mini Kit with manufacturer protocols (Qiagen Inc., Hilden, Germany), but for the final elution step, I used 120 µL of buffer after a 5-min. incubation. Every extraction set had a negative control, and each set was 12–13 samples. The negative controls contained only reagents for quality control, to guard against cross-contamination (Waits and Paetkau 2005). Extracts were then stored at 4°C.

RESULTS

Density, area, and placement of latrines

Over all 4 road surveys, I identified 192 unique latrine sites at El Sauz, 112 at Santa Rosa, and 97 at Russell. Of the 401 unique latrine sites detected, 15% were detected in all 4 surveys (October

2017–May 2019). Excluding the latrines that were only present in Spring 2019, there were 351 unique latrine sites detected, 113 (32%) were only detected in 1 survey, thus persisted <6 months. It was time-consuming to record all single nilgai piles that did not form latrines due to the sheer abundance. After the Fall 2017 survey, I only recorded latrines. I detected 72 non-latrines (<5 fecal piles in 1 m²) in Fall 2017, and only 9 (13%) non-latrines were detected as latrines in the Spring 2018 survey. Latrines were abundant in all road surveys, with higher densities during 5 of 6 Spring surveys in Spring 2018 and Spring 2019 for El Sauz and Santa Rosa (Fig. 2.4).

Average area (\pm SD) of road latrines were similar between sites; 5.5 ± 4.0 m² at El Sauz, 4.7 ± 3.0 m² at Santa Rosa, and 4.2 ± 3.6 m² at Russell. Latrines ranged from 0.2– 42.4 m². The greatest maximum height was 18 cm, $\bar{x} = 5.10$ cm. Almost all latrines detected (>78%; Table 2.1) were in use (fresh or intermediate feces) during a given survey period. Some latrines classified as old in Fall 2017–Fall 2018 (29 at El Sauz, 3 at Santa Rosa, and 16 at Russell), were active in subsequent surveys (90% El Sauz, 67% Santa Rosa, and 56% at Russell). The average distance between road latrines (\pm SE) at El Sauz was 180 ± 10 m (range 3–2,043 m), Santa Rosa = 352 ± 23 m (1–2,583 m), and Russell = 108 ± 6 m (range 1–431 m).

Overall, 28% of road intersections ($n = 139$) had latrines, 24% at El Sauz ($n = 42$), 20% at Santa Rosa ($n = 60$), and 46% at Russell ($n = 37$). Road latrines occurred in 16 vegetation classes, with similar proportions to available vegetation classes (Fig. 2.6).

For the off-road surveys, I recorded 68 latrines and 1,039 fecal piles (non-latrines; Table 2.2). Densities of on-road latrines were greater than off-road for all 3 sites (Table 2.2). The average off-road mean latrine area (\pm SD) of 6.0 ± 2.9 m² ($n = 68$), were similar to on-road latrine mean area (\pm SD) of 5.7 ± 3.5 m² ($n = 287$) for Spring 2018. All transect groups had single

nilgai fecal piles observed, but not all had latrines. The spiny aster wetland community at Santa Rosa, and the grassland community at Russell had no latrine detections. Through distance sampling, I estimated off-road latrines per ha (\pm SE) for each site: 0.9 ± 0.2 at El Sauz, 0.4 ± 0.1 at Santa Rosa, and 0.8 ± 0.3 at Russell, which equate to $10,206 \pm 1,906$ latrines at El Sauz, $2,655 \pm 621$ at Santa Rosa, and 244 ± 97 at Russell (Table 2.2).

Seasonal frequency, sex, and age classes of nilgai that use latrines

I originally monitored 10 on-road latrines each at El Sauz and Santa Rosa, and 4 on-road latrines at Russell, but some latrines became inactive, thus I moved cameras to active latrines. In total, I monitored 37 active latrines, 17 at El Sauz, 11 at Santa Rosa, and 9 at Russell. Some monitored latrines remained active throughout the entire study period from April 2018–March 2019, including 4 at El Sauz, 9 at Santa Rosa, and 2 at Russell. El Sauz was monitored for 36,024 hours, Santa Rosa for 33,749 hours, and Russell for 13,983 hours. Differences in hours at El Sauz and Santa Rosa were mainly due to camera issues, such as dead batteries or cameras disturbed by cattle.

I recorded 10,101 animal visits (on or near latrines) at on-road latrines, including 1,544 nilgai visits (15%). El Sauz had 5,723 animal visits to latrines (635 nilgai, 12% of total visits), Santa Rosa had 3,749 visits (709 nilgai, 19%), and Russell had 629 visits (200 nilgai, 32%). Sixteen species besides nilgai were observed, including nine-banded armadillo (*Dasypus novemcinctus*), badger (*Taxidea taxus*), bobcats (*Lynx rufus*), domestic cattle, coyotes (*Canis latrans*), white-tailed deer (*Odocoileus virginianus*), domestic dog, feral swine (*Sus scrofa*), collared peccary (*Tayassu tajacu*), red lechwe (*Kobus leche*), ocelot (*Leopardus pardalis*), Eastern cottontails (*Sylvilagus floridanus*), raccoon (*Procyon lotor*), striped skunks (*Mephitis mephitis*), turkey (*Meleagris gallopavo*), and other birds. Besides nilgai, I observed defecations

on latrines by cattle ($n = 3$), coyotes ($n = 19$), and deer ($n = 1$). I recorded sniffing events from cattle ($n = 48$), coyotes ($n = 44$), deer ($n = 27$), feral swine ($n = 12$), collared peccary ($n = 4$), and raccoons ($n = 3$).

On average, a given latrine was visited by a nilgai 0.42 times a day at El Sauz, 0.50 at Santa Rosa and 0.34 at Russell (Fig. 2.7). The frequencies of visits for latrines by latrine area were not consistent among sites. El Sauz Ranch had higher frequencies of visits on small latrines (0.53 visits/day vs. 0.33). Russell had similar visits between small and large latrines (0.38 vs. 0.33), whereas Santa Rosa had higher frequency on large latrines (0.57 vs. 0.40). Overall, small latrines ($n = 19$) which averaged 0.46 visits per day ($n = 641$), were similar to large latrines ($n = 18$) which averaged 0.43 visits per day ($n = 903$). At any given month, I often found a different latrine had the highest frequency of visits, sometimes a latrine would have the highest visitation rates during 1 month and then no visits the next.

There were above average peaks in visitation frequencies for El Sauz in the months of April–June and January–February, Santa Rosa had peaks during August, and December–March, and Russell had peaks during April–June and January–March (Fig. 2.7). Bulls contributed the highest proportion of nilgai latrine visits overall (Table 2.3), and for El Sauz and Santa Rosa, contributing to 74% of El Sauz visits and 75% of Santa Rosa. Russell had similar cow to bull proportions (42% cows vs 38% bulls, rest unknown or calves). Subadult bulls were rarely detected, and contributed to 6% of visits at El Sauz, 3% at Santa Rosa, and 18% at Russell. All age and sex classes defecated on latrines, with 147 defecations at El Sauz, 180 at Santa Rosa, and 29 at Russell (Fig. 2.8). Nilgai latrine defecations averaged once every 10 days at El Sauz, 12 days at Santa Rosa, 20 days at Russell, and averaged every 12 days overall. There were 356 defecations, with 329 bulls (92%, only 1 subadult bull), 20 cows (6%), 6 calves, and 1 unknown.

Of the 20 cow defecation events, 13 (65%) had bulls visiting by the following day, 9 of which bulls visited within 15 hours of the defecation. There were 5 of the cow defecations that received defecation from bulls by the next day. For 2 of these events, the cow was with a bull when she defecated, and 1 bull defecated immediately following the cow. Sniffing events occurred from all sex and age classes, with 178 events at El Sauz, 348 at Santa Rosa, and 37 at Russell. Bulls contributed to 81% of the sniffing events at El Sauz, 87% at Santa Rosa, and 37% at Russell. Nilgai sniffing events occurred at similar frequencies to defecations, averaged 8 days El Sauz ($n = 178$), 6 days Santa Rosa ($n = 348$), 16 days Russell ($n = 37$), and 7 days overall ($n = 563$).

The lowest proportion of the nilgai latrine visitations were during mid-day and mid-afternoon (1400–1659 hr, 12%, Fig. 2.9). Nilgai cows had higher proportions of visitation from early-morning to mid-day (0500–1359 hr) than bulls thus the bulls had higher proportions of visitations from evening–night (1700–0459 hr; Fig. 2.9). Most (75%) of the nilgai bull defecations occurred during the evening–night (1700–0459 hr; Fig. 2.9).

I noticed other behavioral responses of nilgai at latrine sites besides defecation and sniffing. I documented 5 cases of nilgai bulls showing flehmen responses (Fig. 2.10), bulls with raised tails displacing other bulls (2), bulls tending cows, 3 cases of bulls rubbing their head in vegetation near latrines (Fig. 2.11), 1 cow urinating on a latrine as a bull licked her urine and showed a flehmen response, 1 active mating display, and 2 possible matings, with both sexes showing erect tails at latrines. One bull fight occurred around a latrine. Both bulls circled the latrine and one urinated and defecated during the dispute. The bulls showed signs of fresh wounds. Cows and calves were documented defecating on the latrine 4 days earlier. Both of the bulls were photographed previously defecating at that latrine, and after the fight both males still defecated on the latrine, but at different times.

Individual nilgai use of latrines via DNA analysis

Few nilgai bulls were individually recognizable, though physical characters such as horns, scars, or pelage could identify some individuals. Therefore, genetic analyses were needed to confirm identity of latrine visitations. I collected 114 samples from 15 latrines. I extracted 75 samples from latrines that had more than 2 defecation events.

I identified 7 genetic markers that amplified in nilgai that were sufficiently variable to identify individuals: BM415, BM4208, ETH152, BovPRL, BM848, ILSTS, OCAM, and sex determination marker S4B. I used a 16- μ L PCR volume for each sample, including 8.0 μ L AmpliTaq Gold $\text{\textcircled{R}}$ 360 PCR master mix (Taq DNA Polymerase, dNTPs, 3.5 μ L double-deionized H₂O, 1.0 μ L bovine serum albumin (2 mg/mL BSA; Thermo Scientific, Waltham, MA), 0.1 μ L for each forward and reverse primer at 100 μ M (10 pmol), and 1.5 μ L DNA extract. I included negative controls during extraction and PCR to verify absence of contamination. I amplified the selected markers after empirical optimization of the PCR protocols.

The thermocycling conditions for BM415, BM4208, BovPRL, and ETH152 had initial denaturation of 94°C for 10 minutes, 10 cycles 94°C for 30 sec, within-cycle decreasing annealing temperature for 62°C, 61°C, 60°C, extension of 72°C for 60 sec, 40 cycles at 94°C for 30 sec, 54 or 58°C annealing temp. for 90 sec, and 72°C for 60 sec, and a final extension of 72°C for 30 min. Marker conditions were the same for BM848, but starting at a 61°C decreasing annealing temperature, ILSTS had a 59°C starting decreasing annealing temp., and OCAM had a 60°C starting decreasing temp. The thermocycling conditions for the sexing marker S4B were the same except with a 62°C starting decreasing temp., annealing temp. of 52°C for 45 seconds. All markers were run through PCR separately, but pooled into 2 panels before loading onto an ABI 3130x1 DNA sequencer for separation and detection. Panel 1 included BM415, BM4208,

BM848, and ETH152; I mixed 2 μ L of each PCR product and combined 1 μ L of the mixture with formamide and an internal size standard, as recommended by the manufacturer. Panel 2 consisted of BovPRL, ILSTS, OCAM, and S4B; I prepared the mixture for loading onto the sequencer in the same manner. I quantified fragment sizes and allele bins using the software GeneMapper 4.0. I genotyped all heterozygotes ≥ 2 times and all homozygotes ≥ 3 times to account for the potential of allelic dropout, failed amplification, and false alleles (Taberlet et al. 1999, Broquet et al. 2007).

Only 25 samples were able to be genotyped to individuals at ≥ 4 loci from 9 different latrines, one latrine only had 1 successful genotyped sample. For the successfully genotyped samples, there were 20 males and 5 females. Of the genotyped samples, 10 were only a few hours post-defecation (classified as #1 freshness), 14 were classified as #2 fresh, and 1 was #3 fresh. The S4B sexing marker amplified well, and I was able to sex 57 samples, 51 males (89%) and 6 females (11%). Photographs of defecation events indicated several repeated defecations from the same individuals (Table 2.4). In 50% of the cases from January–February 2019, latrines were defecated on by a single individual old adult bull, though in one case, a latrine was defecated on by 2 different old adult bulls, one distinguishable because it was ear-tagged (Table 2.4).

Field observations

Throughout this study, I recorded noteworthy field observations. In Chapter III, I identified fence crossings sites, or openings beneath fences created by wildlife. At El Sauz Ranch I identified 34 fence crossing sites, and 50% had at least 1 latrine present, but often had 1 on both sides of the fence a few meters from the crossing sites. I observed similar latrine placement at a gated-off

bridge. There was a latrine on both sides of the bridge. During the road surveys, I also documented latrines established within large road pot-holes and depressions.

I documented latrines placed near skeletons of nilgai, cattle, and deer, as well as nilgai carcasses. One nilgai bull died after becoming entangled in a fence, and 2 weeks later large latrines formed on both sides of the fence. I observed 3 accounts of dead nilgai bulls near fences. At Santa Rosa, within a few weeks, a latrine formed next to the carcass; a randomly assigned camera was placed on this latrine showing a mature bull visiting and defecating on the latrine. When this carcass was dragged into the brush from scavengers, a latrine formed where the skeleton laid. Two nilgai bulls died at El Sauz about a month apart, and the carcasses were within 20 m of each other. This was on a road intersection near the fence, and a massive 42 m² latrine (scattered in density) formed near these 2 bulls. During the off-road surveys, I observed a latrine around a deer skeleton and a second latrine around a cattle skeleton. A nilgai harvest took place at El Sauz in July 2018, and the processing site was next to a latrine I was monitoring. Prior to the harvest, nilgai cows, calves, and bulls used the latrine that was located in a wide-open gravel area. After the harvest, activity nearly ceased at this latrine, but approximately 50 m away where the processing occurred, a latrine formed immediately following the harvest, which still persisted in March 2019.

DISCUSSION

Jarman (1974) grouped antelope species into 5 classes based on their social behaviors and organization. While nilgai antelope were not included in his paper, nilgai fit into class C based on their ecology. Nilgai are strongly sexually dimorphic (Sheffield et al. 1983), males can be found singularly or in bachelor groups, there are cow-calf groups (Fall 1972, Singh 1995), and some males have strong, tight home ranges while others are much larger (Qureshi 1991, Foley et

al. 2017). Also, nilgai are intermediate feeders (Sheffield 1983, Singh 1995, Hines 2016), which fits into class C. Jarman (1974) observed that antelope species in this class often have a “proportion of adult males that obtain exclusive mating rights by possession of a demarcated piece of ground without having permanent ownership of females.” Territorial male antelope will also evict young males from female herds, causing male bachelor groups to form (Jarman 1974). Furthermore, Foley et al. (2017), reported a young female nilgai made the longest dispersal. This dispersal of young females from an area has been observed in dik-dik, when either the territorial male or the female parent forces the female offspring to disperse (Hendrichs and Hendrichs 1971). Territoriality is common amongst species of antelope, and especially displayed through urination and defecation (Dasmann and Mossman 1962, Estes 1967, Jarman 1979). With the lack of research on nilgai behaviors, the extent of territoriality and social behaviors in nilgai is unknown. The results of my study on nilgai latrine ecology help illustrate the important role latrines serve for social communication and territoriality.

Nilgai latrine use was dynamic. I found latrines were abundant on roads, and had greater densities and mean area during spring surveys vs. fall. The peak in nilgai breeding occurs between December–March (Fall 1972, Sheffield et al. 1983), between the fall and spring surveys. Other species have shown increased rates of defecation on latrines during breeding seasons or female receptivity (Dunbar and Dunbar 1974, Novellie et al. 1984, Kranz 1991, Roberts and Dunbar 2000). Foley et al. (2017) found males at El Sauz to have elevated movement rates during December, while females increased movement rates during June–August. A change in available food resources also might influence the density of latrines, especially if latrines serve a territorial function; territories may be abandoned or moved dependent on the

resources (Jarman 1974, 1983). I predict densities of latrines may also change if territorial males are harvested.

About a third (32%) of latrines documented were used for <6 months, but 15% lasted from Fall 2017–Spring 2019, despite heavy rainfall events and periodic road maintenance that cleared latrines. The trend of latrines disappearing affected camera monitoring of latrines. I had to move latrine cameras 7 times at El Sauz, 1 time at Santa Rosa, and 5 times at Russell because a latrine received no nilgai defecations for >4 weeks. Most latrines classified as “old” were used again in subsequent surveys. Thus, latrines can go long periods of time without use, but nilgai often re-form latrines at the same locations, which indicates that physical location of latrines is important. The shift in latrine dynamics might be due to changes in nilgai social dynamics, or changes in water and food resource distribution, but I was unable to evaluate these hypotheses.

Road latrines were found in pairs as little as 1 m apart, or separated by up to 2,583 m. Latrines were common on intersections and unpaved roads. Fall (1972) also frequently observed nilgai latrines at intersections of roads or trails in South Texas. Most vegetation communities had road latrines, and this distribution of latrines was represented in off-road surveys as well. While the off-road surveys had lower densities of latrines than on-road, both had high latrine densities, which equate to hundreds to thousands of latrines on these study sites. The latrine densities were higher than nilgai densities at El Sauz and Santa Rosa, indicating individual nilgai must use multiple latrines. Santa Rosa Ranch had similar nilgai population densities to El Sauz, but had the lower latrine densities. Thus, estimates of population densities were not directly comparable to latrine densities. Piles from single defecations were also abundant, showing defecations are not restricted to latrines. While I found placement of latrines to be important to nilgai, it is

unknown to whether locations of single defecations serve a specific function for social communication.

Roads, intersections, pot-holes in roads, bridges, sand dunes, and fence lines, are typically areas of high visibility. Nilgai tend to move through or along these areas often, specifically trails and fence crossings, and these areas often serve as common locations for territorial animals to place latrines (Black-Decima and Santana 2011, Chapter III, Wronski et al. 2013), since conspecifics may be more likely to encounter the latrines (Black-Decima and Santana 2011). Schaller (1967) suggested the exaggerated, long held, posture that nilgai display during defecations may visually serve a social function as well. Nilgai appear to select for these areas of high movement and visibility for latrine placement. In addition, if latrines are visited more frequently at borders to other territorial rivals, then this combination of placement to increase encounters from neighbors and increased visitation rates would signify nilgai latrines function for maintenance of territorial borders (Gosling 1986, Smith et al. 1989, Johansson and Liberg 1996).

Latrine usage differed by nilgai sex and age classes. Bulls contributed to most of the latrine visits (70%) and defecations (89% DNA samples, 92% in photos). I documented only 1 photograph of a subadult bull that defecated on a latrine, but several visits with subadult bulls sniffing latrines. Latrines were mainly visited and defecated on by one or few bulls at night. The use of latrines from old adult bulls is one indicator that territorial bulls use latrines. Territorial male animals tend to be larger, better fighters, and are typically the dominant males of social groups (Jarman 1974). These “old” nilgai bulls have thick necks and thick skin on the neck, which could be beneficial since nilgai are the only bovid species which bulls display neck-fighting (Walther 1974, Sharma and Rahmani, 2004). For impalas, the males with significantly

larger necks correspond to male territoriality, with non-territorial males having smaller necks (Jarman 1979). Since latrines were mainly used by adult bulls, and the one bull fight at a latrine involved defecations before, during, and after the fight, it suggests latrines serve as a dominance or threat function for bulls (Ralls 1971, Barrette 1977, Moehlman 1985). Further research on how home range sizes compare to latrine distribution would help confirm if nilgai show territory or resource defense. Both male and female nilgai commonly have large home ranges (571–29,909 ha; Qureshi 1991, Moczygemba et al. 2012, Foley et al. 2017), but some adult bulls have comparatively small home ranges (Qureshi 1991, Foley et al. 2017), presumably dominant males (Qureshi 1991). Spinage (1969) found male waterbuck (*Kobus defassa ugandae*) may be evicted to smaller territories after losing a fight. The rank of the nilgai bulls in small territories is unknown, and requires further attention. Mating strategies vary between species in which territorial males place latrines to mark small territories, as seen with polygynous white rhinoceros (White et al. 2007) and facultative monogamous or sometimes temporarily polygamous dik-diks (Roberts and Dunbar 2000). Nilgai are polygynous (Leslie 2008), but further research is needed to address whether nilgai bulls monopolize more than one female at a time.

The scent-marking behavior of many species of antelope involves rubbing the ground or nearby vegetation with their forehead or horning the ground near latrine sites (Dorst and Dandelot 1970, Jarman 1974, Brashares and Arcese 1999). This is a common behavior for nilgai's closest relative, the four-horned antelope (Sharma et al. 2009). The horning behavior was observed by Oguya and Eltringham (1991) from a captive nilgai bull. The rubbing could be of secretions from the pre-orbital gland, which provides sex specific pheromones (Ralls 1971). Fall (1972) predicted nilgai were unlikely to scent-mark with preorbital glands because of the small

size of their glands. My documentation of 3 events with nilgai bulls rubbing vegetation next to latrines may provide evidence to the contrary. For impalas, this behavior is associated with territorial marking for males (Jarman 1979). Another common behavior for animals that use latrines is scraping the ground near the latrine (Hendrichs 1975, Wronski and Plath 2010). Sometimes species scrape off previous defecations to mask odors, display mate-guarding behaviors, or to challenge other males (Hendrichs 1975, Brotherton 1994). I did not document scraping behavior in nilgai, though faster photo bursts might be needed to detect scraping behaviors.

Most (54%) nilgai visitations had nilgai acknowledge the latrines by defecating or sniffing. At a finer scale, I noticed bulls that would not defecate only sniffed the latrine and would not step foot on the latrine. Typical photographs of defecations from bulls involved bulls with all 4 feet on the latrine defecating on the center of the latrine, a behavior that might relate to dominance status or territorial marking (Marneweck et al. 2018). I did not classify placement of defecations in conjunction with photographs, so further research could be done to understand how defecations are placed within a latrine that is used by multiple individuals. Cows would occasionally just walk over the latrine with no acknowledgment of it. I did not observe this behavior in males.

Cows would visit latrines on occasion, sometimes in cow-calf groups. Only 20 defecation events (6% of total nilgai defecations) occurred from cows, but over half ($n = 13$, 65%) resulted in a visit from a bull by the following day. Since photographs of nilgai bulls showed flehmen responses (1 as a cow is urinating on a latrine), a bull fight at a latrine a few days after a cow defecated on it, 1 mating, and several bulls tending cows, I suggest cows used latrines to advertise reproductive receptivity. There were increased visitation rates during the typical peak

in the nilgai breeding season, which also suggest a reproductive receptivity function. For klipspringer, females may increase marking rates when they are receptive, thought to be a strategy of females to promote male competition (Roberts and Dunbar 2000). The bull fight documented around the latrine 4 days after a cow-calf group defecated provides support for a female-driven male competition for mating rights. My results do not provide evidence for nilgai cows to have a territorial or intra-group communication function for latrines. Overall, the number of female defecations and visits were low in this study. Nonetheless, I estimate hundreds to thousands of latrines occur on these study sites, so there may be latrines that are used differently by cows. Since nilgai have large home ranges (Moczygemba et al. 2012, Foley et al. 2017), the maintenance of latrines on home range boundary would be inefficient, so nilgai may maintain latrines at home range centers (Gosling 1981, Roberts and Lowen 1997, Jordan et al. 2007, Wronski et al. 2013). If females of the same social group exclusively defecate on a latrine, then intra-group communication could be a function of nilgai cow latrine use (Dröscher and Kappeler 2014).

There were 16 non-target species that visited latrines, and occasionally there were defecation events from cattle, coyotes, and white-tailed deer. There is a lack of literature on the purpose of multiple species use of the same latrine, but cattle, coyote, and deer do not create latrines. Coyote will defecate or urinate as a response to olfactory stimuli (Turkowski et al. 1979), and I assume cattle and deer responded to the olfactory stimulus as well.

My fecal DNA analysis produced mixed results due to low quality and quantity of DNA, where I was unable to identify individuals consistently. However, the genetic results did mirror the camera data in that most of the defecations were males, with a few repeated visits from the same males. Some antelope species use latrines as a function of mate-guarding, for

advertisement of the male's ability to defend females for mating privileges from other males (Roper et al. 1986). It would be beneficial to investigate the number of latrines an individual cow will defecate-urinate on, and whether the cow selects for a particular individual bull's latrine to defecate on. Maybe nilgai cows would defecate on latrines shared by more than one bull more frequently to elicit competition among males.

Overall, latrine placement and use was dynamic, suggesting that latrines are an important aspect of nilgai communication and structure. The increase in latrine densities, area, and visitation rates related to an increase in nilgai reproductive receptivity. Latrines were almost exclusively defecated on by a few individual bulls, mostly the large-bodied "old adults," and cow defecations often attracted a response from a male nilgai by the following day. My evidence suggest nilgai bulls are territorial, and additional information on latrine placement and visitation rates in relation to location within territories and to neighboring bulls could indicate bull latrine function may be for border maintenance and scent-marking as well. This is the first latrine ecology study on nilgai, and one of the few studies ever published on nilgai social behavior.

MANAGEMENT IMPLICATIONS

Nilgai-human conflicts are increasing in Texas, India, Nepal, and Pakistan, due to their ability to spread cattle fever ticks in Texas (Pérez de León et al. 2012) and extensive crop damage in India, Nepal, and Pakistan came their native range (Kahn 2014). My study is the first to investigate nilgai latrine behavior, and one of the few studies on nilgai antelope. It uncovers the importance of latrines for nilgai social communication in regards to social structure and reproduction. My results support territorial behavior of nilgai bulls, and territoriality can have a significant influence on population structure and dynamics (Adams 2001). Nilgai latrines are discrete locations that are regularly re-visited; therefore, latrines might be used for implementation of tick

treatments. This strategy would be most effective if latrines were used by multiple individuals. Unfortunately, given the abundance of latrines, the variability in duration, and near-exclusive use by one or few individuals, latrines would not serve as ideal locations to target nilgai for disease control. Latrine densities on unpaved ranch roads may serve as an index to nilgai population density or age structure, though this should be interpreted with caution because I did not observe a strong correlation with population estimates over the range of population sizes on my study sites. Latrines may relate to bull territory size or location, but further research is needed on nilgai latrine use in relation to home ranges and territories. It would be ideal to conduct a genetics study on individual distribution of latrines to investigate defecation rates of individuals in relation to territories, but would be difficult with the low quality of the fecal samples. Nilgai are variable in their latrine defecations, but averaged 1 defecation every 12 days, which makes collection of quality samples difficult, unless there were daily latrine checks for collection of samples. This question on individual distribution of latrines would be better addressed using marked nilgai and camera traps. Ideally, cameras on two sides of the latrine would assist in identifying individual nilgai. Overall, this study helps reveal insight of the elusive nilgai antelope, providing a basis of information to understand of their complex social behaviors, that in turn help establish better management strategies.

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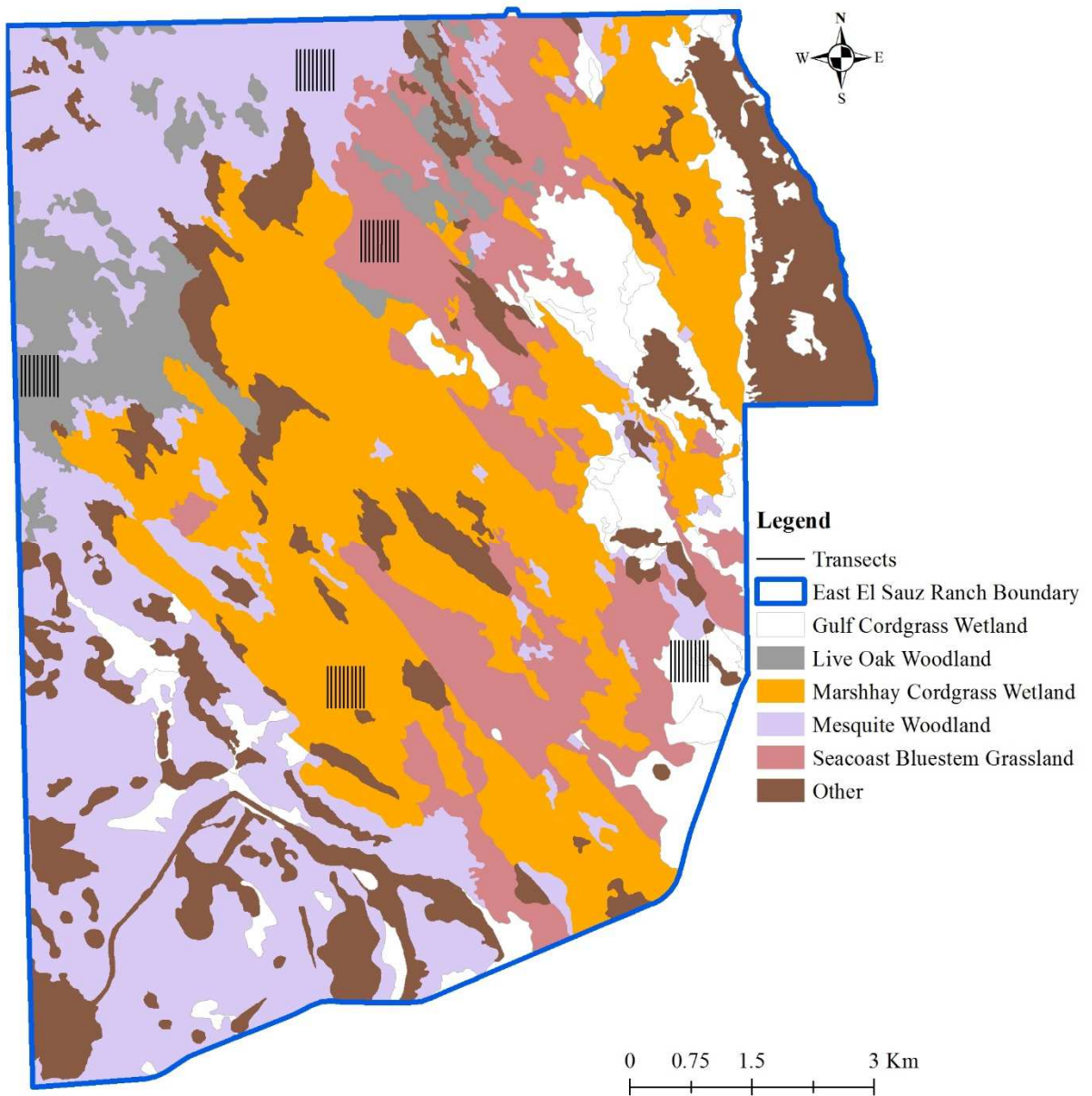


Figure 2.1. Location of transects used to estimate nilgai antelope latrines off-road at the East Foundation’s East El Sauz Ranch (10,984 ha) near Port Mansfield, Willacy County, Texas, during Spring 2018. Each of the 5 major vegetation communities received 10 500-m transects.

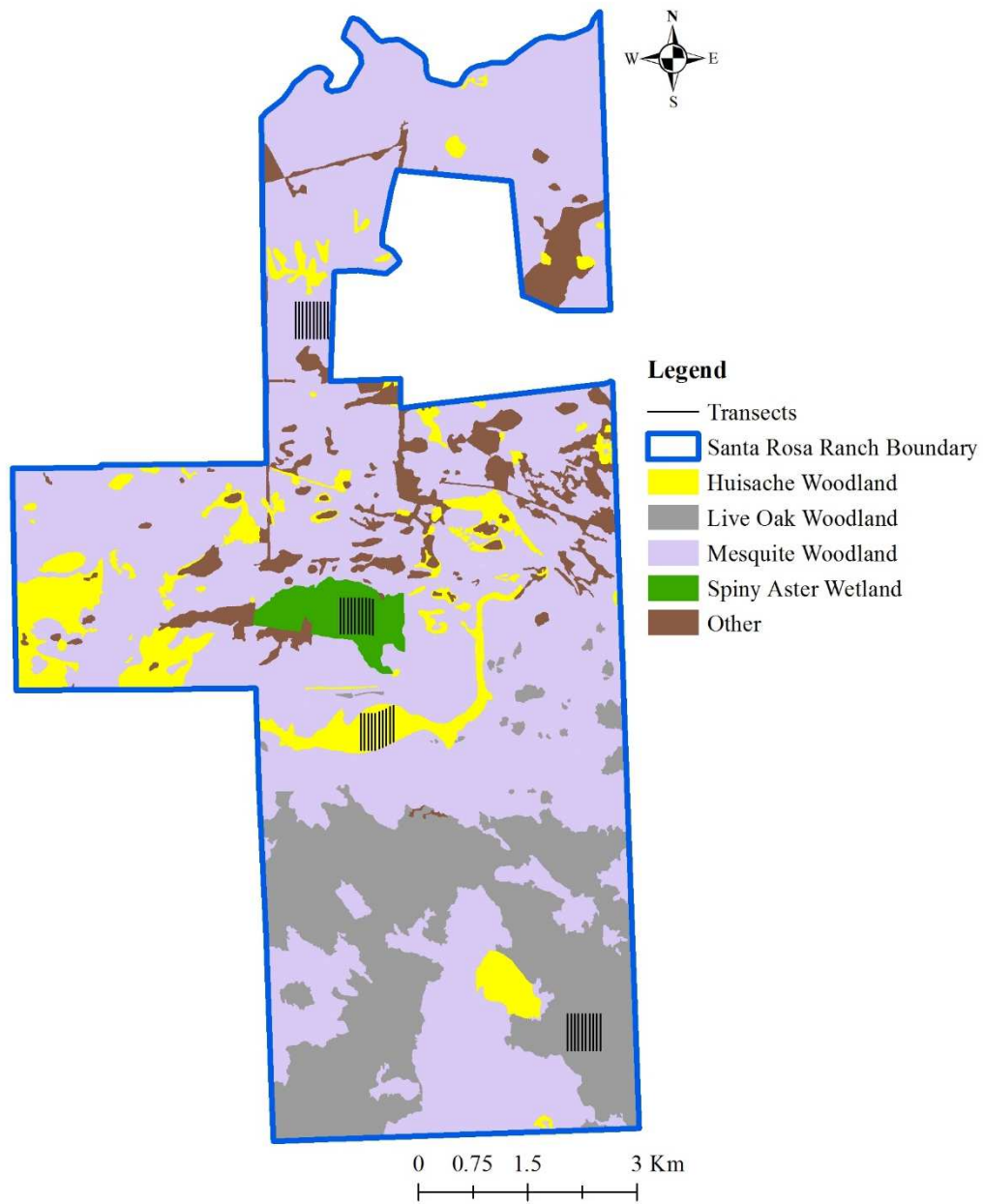


Figure 2.2. Location of transects used to estimate nilgai antelope latrines off-road at the East Foundation' Santa Rosa Ranch (9,000-ha) near Riviera, Kenedy County, Texas, during Spring 2018. Each of the 4 major vegetation communities received 10 500-m transects.

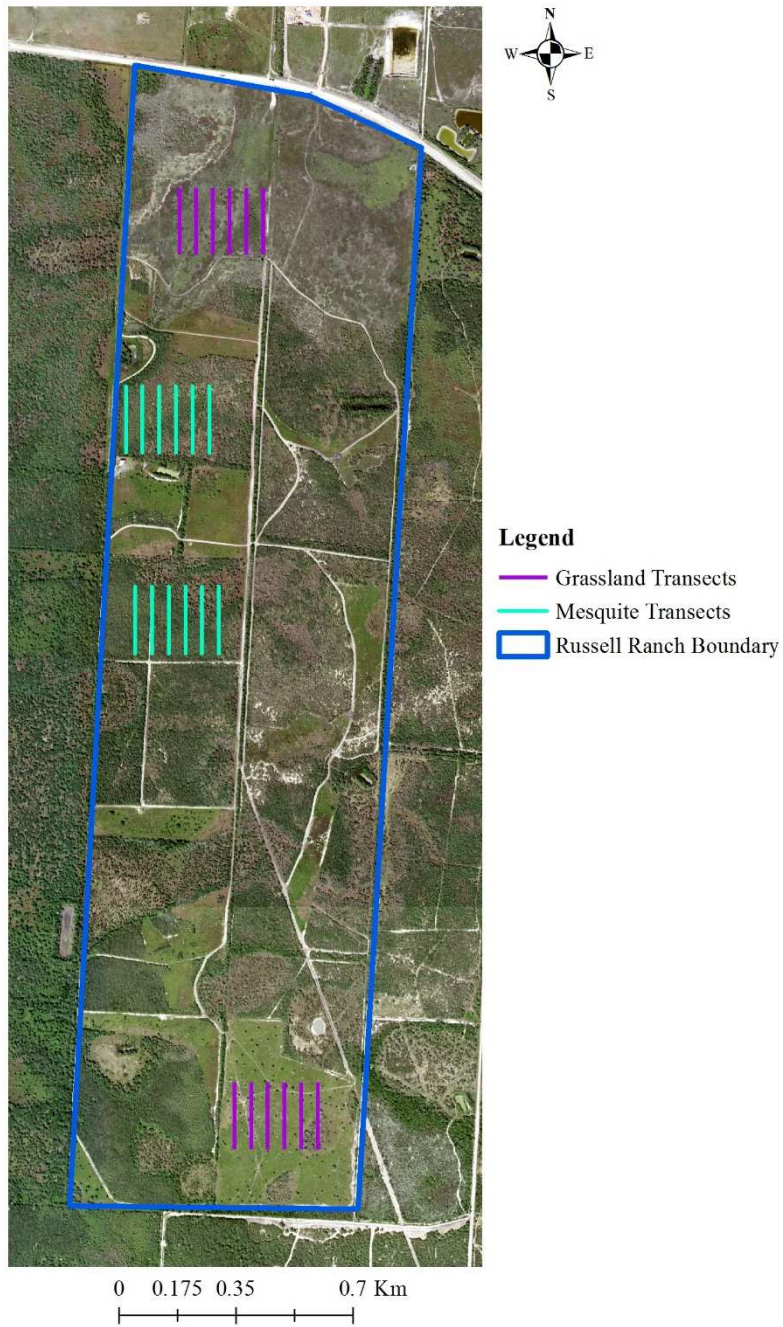


Figure 2.3. Location of transects used to estimate nilgai antelope latrines off-road at Russell Ranch (289 ha) near Rio Hondo, Cameron County, Texas, during Spring 2018. Twelve 200-m transects were located in both grassland and mesquite thornscrub communities.

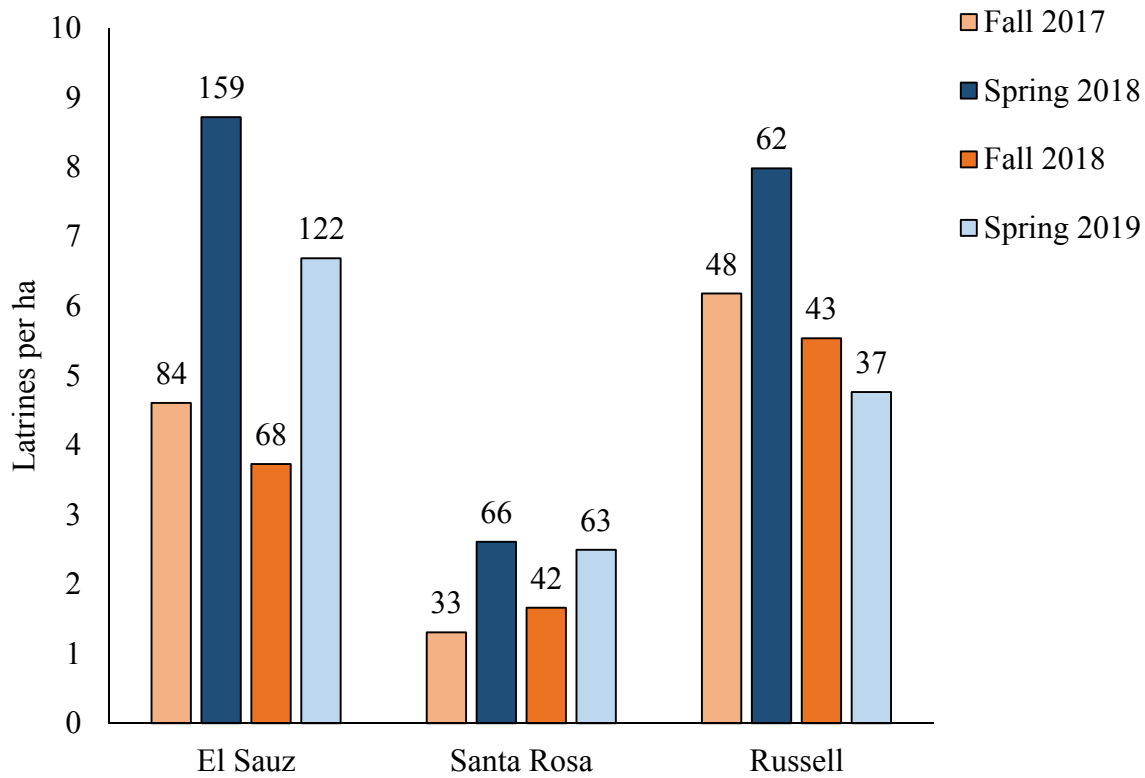


Figure 2.4. Density of nilgai latrines on unpaved roads at the East Foundation’s El Sauz and Santa Rosa Ranches, and Russell Ranch in South Texas during Fall 2017, 2018, and Spring 2018, 2019. Surveys were complete counts of latrines assuming a fixed 5 m width. The number of latrines identified are labels above bars.

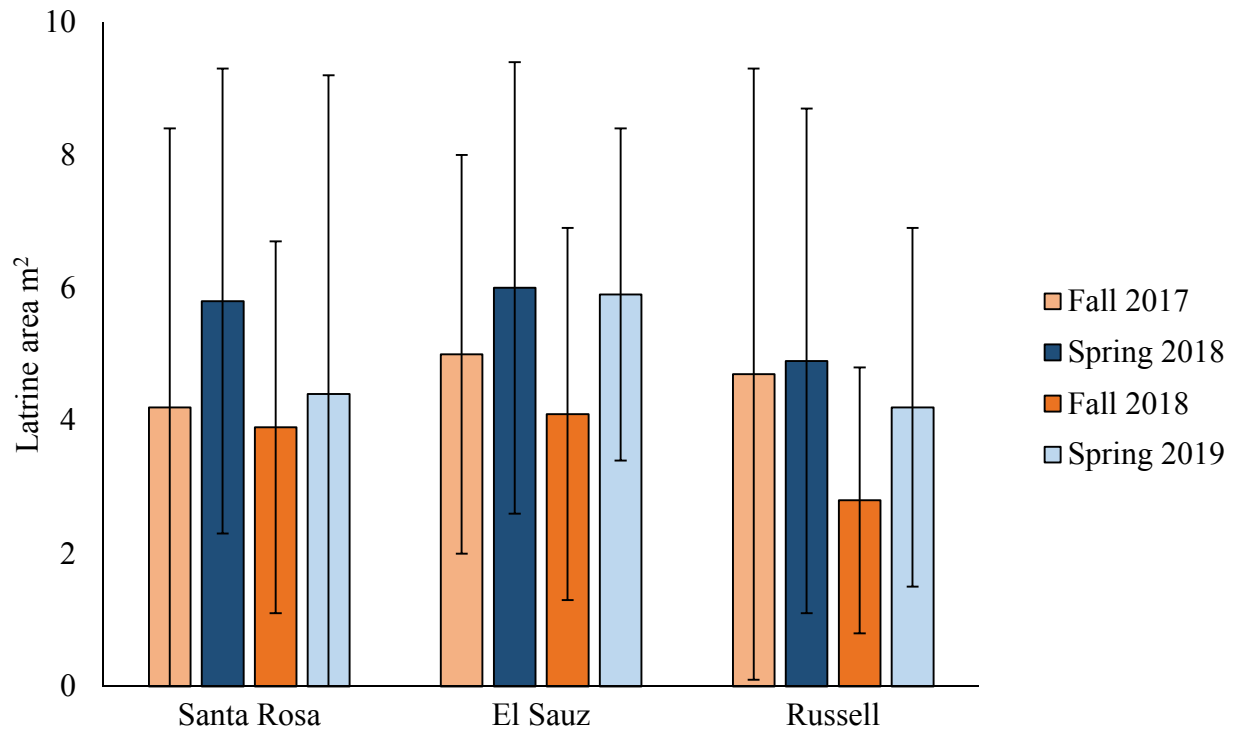


Figure 2.5. Spatial area (length \times width) of nilgai antelope latrines on unpaved roads ($m^2 \pm SD$) at the East Foundation’s El Sauz and Santa Rosa Ranches, and Russell Ranch, South Texas, calculated from surveys during Fall 2017, 2018, and Spring 2018, 2019).

Table 2.1. Proportion of active nilgai latrines (fresh or intermediate feces) on unpaved roads at the East Foundation’s El Sauz and Santa Rosa Ranches, and Russell Ranch in South Texas for each of 4 survey periods (Fall 2017, 2018, and Spring 2018, 2019). Surveys were complete counts of all latrines encountered.

Active latrines				
Surveys	El Sauz	Santa Rosa	Russell	Overall
Fall 2017	83%	91%	81%	84%
Spring 2018	94%	100%	94%	95%
Fall 2018	91%	100%	93%	94%
Spring 2019	92%	97%	78%	91%
Overall	91%	98%	87%	

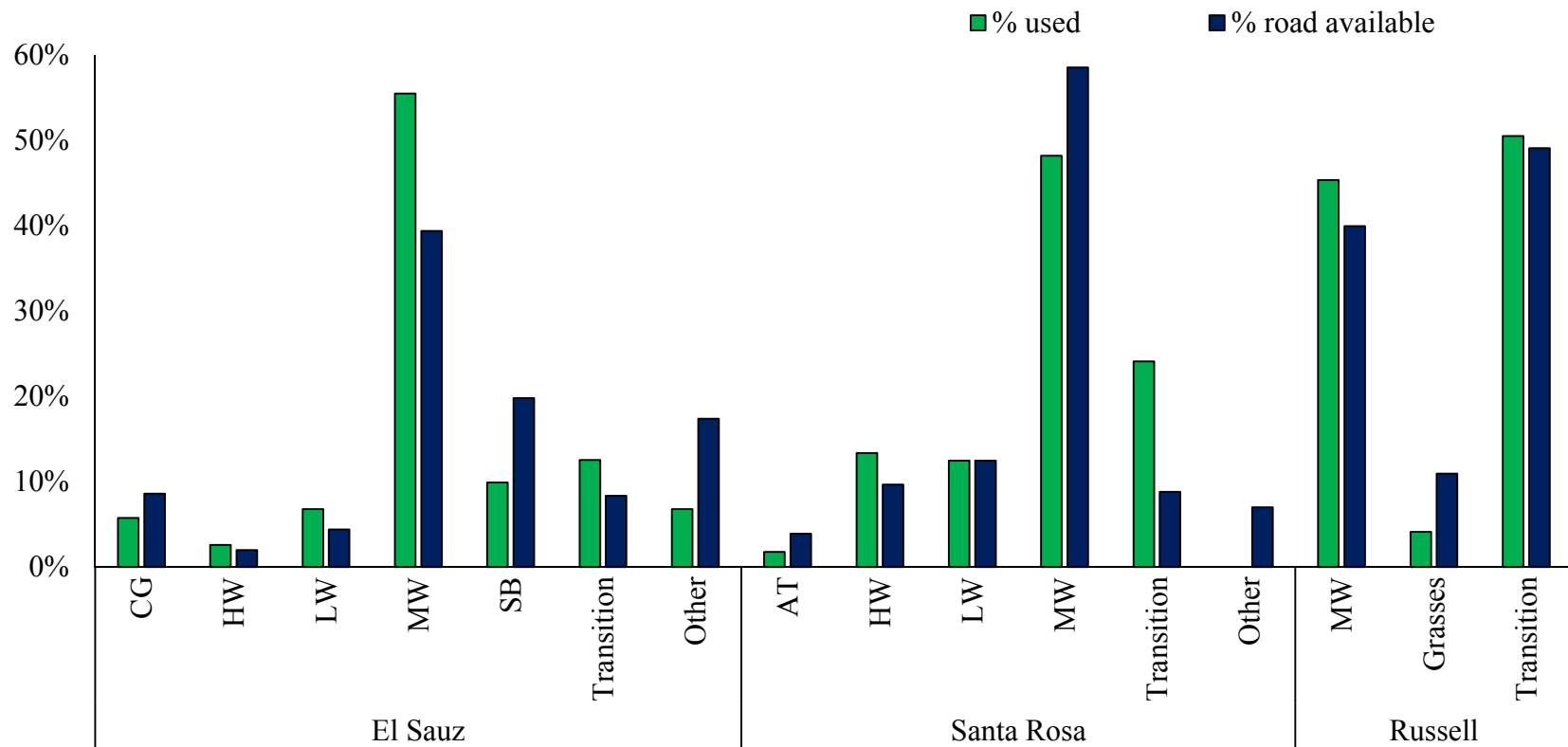


Figure 2.6. Location of Nilgai antelope latrines encountered on unpaved roads by vegetation communities at the East Foundation's El Sauz and Santa Rosa Ranches, and Russell Ranch in South Texas from Fall 2017–Spring 2019. Surveys were complete counts of all latrines on roads, and included 192 latrine locations at El Sauz, 112 at Santa Rosa, and 97 at Russell Ranch. Vegetation communities included: gulf cordgrass grassland (CG), huisache woodland (HW), live oak woodland (LW), mesquite woodland (MW), seacoast bluestem (SB), arrowfeather threeawn (AT), grassy areas dominated by guinea grass (Grasses), and roads that separated vegetation communities (Transition).

Table 2.2. Densities of nilgai antelope latrines on- and off-road (\pm SE) for the East Foundation's El Sauz and Santa Rosa Ranches, and Russell Ranch in South Texas during Spring 2018.

Location	Sites		
	El Sauz	Santa Rosa	Russell
On-road ^a latrines/ha ($n = 287$)	8.7	2.6	8.0
Off-road ^b latrines/ha ($n = 68$)	0.9 ± 0.2	0.4 ± 0.1	0.8 ± 0.3
Off-road ^b ha surveyed	100	80	19.2
Latrine estimate ^{bc}	$10,206 \pm 1,906$	$2,655 \pm 621$	244 ± 97

^a Complete counts of latrines encountered assuming a fixed 5-m road width per site

^b Identified through distance sampling surveys in major vegetation communities on each site

^c Total number of latrines estimated per site

Table 2.3. Number and proportion of age-sex classes of nilgai antelope from latrine visits during April 2018–March 2019, from the East Foundation’s El Sauz and Santa Rosa Ranches, and Russell Ranch in South Texas. Data were collected from 24 latrines monitored with camera traps.

Age class	Visits	Proportion of Total
Adult Females	257	17%
Subadult Females	73	5%
Old Adult Males	611	40%
Adult Males	405	26%
Subadult Males	59	4%
Calves	87	6%
Unknown	52	3%
Total	1,544	

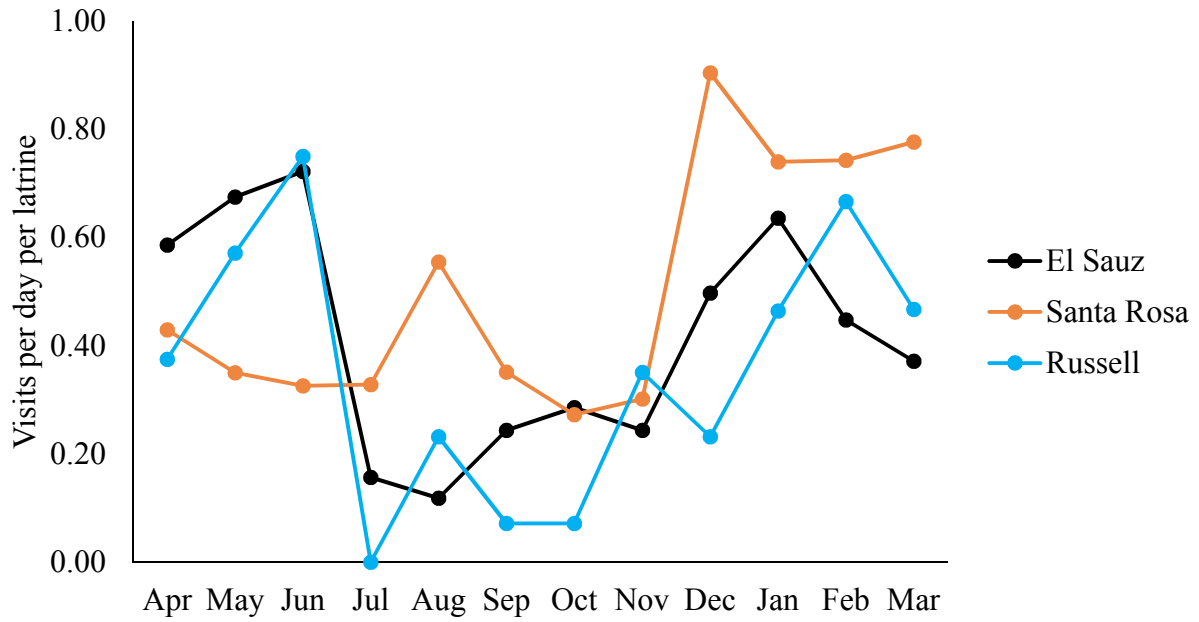


Figure 2.7. Average visits per day at nilgai antelope latrines at the East Foundation’s El Sauz and Santa Rosa Ranches, and Russell Ranch in South Texas during April 2018–March 2019. Visits were recorded by trail cameras for 2 weeks of each month (10 cameras at El Sauz, 10 at Santa Rosa, and 4 from Russell Ranch).



Figure 2.8. Nilgai antelope bull defecating on a latrine, with a typical placement of all 4 feet on the latrine, at the East Foundation's El Sauz Ranch near Port Mansfield, Willacy County, Texas, during October 2018.

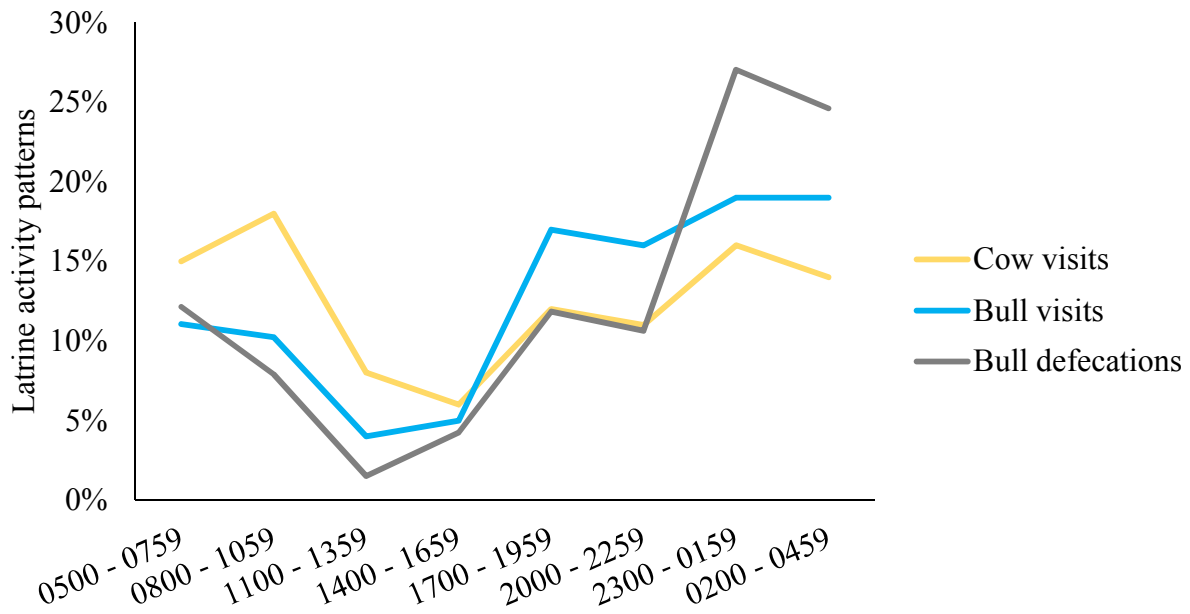


Figure 2.9. Activity patterns of nilgai antelope visits by sex and number of defecations at latrine sites at the East Foundation’s El Sauz and Santa Rosa Ranches, and Russell Ranch in South Texas during April 2018–March 2019. Camera traps revealed 330 cow visits, 1,075 bull visits, and 329 bull defecations. Cow defecations were rare ($n = 20$) and are not included. Times were categorized into 3-hour segments of the day.



Figure 2.10. Nilgai antelope bull displaying flehmen behavior in response to nilgai cow urination on a latrine at the East Foundation's El Sauz Ranch, near Port Mansfield, Willacy County, Texas, February 2019.



Figure 2.11. Nilgai antelope bull with vegetation on horns next to a latrine site at the East Foundation's Santa Rosa Ranch, near Riviera, Kenedy County, Texas, December 2018. This behavior is consistent with scent marking displays from other species of antelope rubbing secretions from preorbital glands on vegetations.

Table 2.4. Defecations on latrines by individual nilgai antelope at the East Foundation's El Sauz and Santa Rosa Ranches, and Russell Ranch from 1 January 2019 through 28 February 2019.

Data were collected from 24 latrines monitored with camera traps; some latrines with no defecations photographed were excluded.

Site	Total defecations ^a	Latrine ID	# defecations ^b	Individual descriptions	% defecations ^c
El	19	E5	13	Old adult bull - ear tagged	68%
Sauz	19	E5	2	Old adult bull - no ear tag	11%
	19	E5	4	Unidentifiable old adult bulls	21%
	6	E25	6	Old adult bull	100%
	12	E96	1	Old adult bull - foot dot	67%
	12	E96	1	Unidentifiable old adult bulls	17%
	12	E96	8	Cow	8%
	12	E96	2	Calf	8%
	2	E100	2	Cow	100%
	3	L152	3	Unidentifiable old adult bulls	100%
Santa	2	S18	2	Unidentifiable old adult bulls	100%
Rosa	1	S19	1	Old adult bull - odd shoulder	100%
	9	S28	2	Old adult bull - lightning scar	22%
	9	S28	7	Unidentifiable old adult bulls	78%

Table 2.4. continued

Site	Latrine defecations ^a	Latrine ID	Individual defecations ^b	Individual descriptions	% defecations ^c
Santa	12	S32	8	Old adult bull - lightning scar	67%
Rosa	12	S32	1	Unidentifiable old adult bulls	8%
	12	S32	1	Cow	8%
	12	S32	1	Male calf	8%
	12	S32	1	Unknown calf	8%
	3	S40	3	Unidentifiable old adult bulls	100%
	3	S59	3	Unidentifiable old adult bulls	100%
Russell	2	R50	1	Old adult bull - sharp horns	50%
	2	R50	1	Cow	50%

^a Number of defecations recorded at the latrine monitored with a camera trap

^b Number of defecations recorded from the individual described at the latrine monitored with a camera trap

^c Proportion individual contributed to overall latrine defecations

CHAPTER III

FENCE LINE ECOLOGY: ANIMAL USE OF FENCE CROSSINGS IN SOUTH TEXAS

ABSTRACT Fences are common throughout the world, but surprisingly, there is limited research on how animals react to fences, especially fences with the purpose of livestock enclosure or marking property boundaries. Previous research on the effects of fencing on wildlife is concentrated on large game animals or long-distance migrators. Wildlife often cross fences at defined fence crossings, since they prefer to go underneath rather than over fences. Fence crossings are areas where the bottom fence wires are pushed up or missing, often with a depression of bare soil beneath. I deployed cameras to monitor 20 fence crossings on net-wire livestock fencing at 2 study sites in South Texas, USA, during April 2018–March 2019. I assessed fence crossing placement and quantified animal usage rates of crossings. Over these 2 sites, I documented 10,889 attempted crossing events, with 58% ($n = 6,271$) of the events successful. Overall, 14 wildlife species, and domestic cattle contributed to crossing events. The average crossing received 3–4 crossing events a day, but this was variable amongst locations. I found larger crossings had higher crossing rates. Peaks in crossing activity corresponded with typical peaks of a species' daily and seasonal movements. Crossing densities and sizes were dependent on the amount of fence maintenance, but crossing locations were often re-established in the same locations after fence repairs. This is one of the first and most extensive studies of all animal species that use fence crossings. Knowledge of contact and movement rates between private landholdings will aid in creation of preventative disease control measures and help us understand the impact of net-wire livestock fencing on animal movement.

KEYWORDS camera traps, connectivity, crossings, fence, fence damage, movement, net-wire fencing, Texas

Humans have the innate talent for building. From houses, roads, bridges, to power lines, anthropogenic features have become customary and often a necessity in today's life. Infrastructure is constantly increasing on the landscape, leading to negative impacts on wildlife worldwide (Forman 2000, Jaeger and Fahrig 2004, Torres et al. 2016, Jakes et al. 2018). Creation of anthropogenic features can lead to loss of wildlife habitat, resulting in declines in wildlife populations (Reijnen and Foppen 1994, Ortega and Capen 1999, Torres et al. 2016). Anthropogenic features can also act as barriers to animal movements by physically blocking access to important resources (Oxley et al. 1974, Williamson and Williamson 1984, Harris et al. 2009), and require increased energy expenditure for animals that try to avoid or traverse the barrier (Dyer et al. 2001, Sawyer et al. 2009, Buchanan et al. 2014, Jacobson et al. 2016). While we are now beginning to appreciate the effects of anthropogenic features on wildlife, it is surprising that fences have received such little attention, far less than roads or powerlines (Jakes et al. 2018).

Fencing has been an integral tool to human society for millennia and the practice is popular throughout the world. Primitive forms of fencing were created thousands of years ago, well before the iconic invention of barbed wire in the American West during the 1800s (Hayter 1939, Hornbeck 2010). Modern fences serve multiple purposes, such as marking property boundaries, confinement of livestock or wildlife, and the reduction of trespassers (Jakes et al. 2018). Fence construction is not often documented or regulated, so the extent of fences in the landscape is unknown and can change with the installation of new fence or removal of old fence (Jakes et al. 2018). Research on fences alone is limited, but even less so on how animals are impacted by fences. Most research on the effects of fences on wildlife focuses on single species (Jakes et al. 2018), typically large ungulates (Scott 1992, Knight et al. 1997,

VerCauteren et al. 2010, ZhangQiang et al. 2013, Burkholder et al. 2018), long-distance migrators (Knight et al. 1997, Jones et al. 2017, Burkholder et al. 2018), and animals facing mortality from fence entanglement (Harrington and Conover 2006). This myopic view has resulted in an almost complete absence of information as to how non-target species are impacted by fences.

Fences impact wildlife movement in direct and indirect ways. As indicated above, migratory species are affected by fences that block movement to obtain water, shelter, or food (Williamson and Williamson 1984, Harris et al. 2009). Fencing could confound predation risk and impede animal escape from predation, as with wolf (*Canis lupus*) kills of Przewalski's gazelle (*Procapra przewalskii*) near fences in China (ZhangQiang et al. 2013), and dog pack kills on white-tailed deer with the assistance of fences (Hölzenbein and Marchinton 1992). Although rare, fence collision mortality with livestock fencing happens with low-flying birds, such as red grouse (*Lagopus l. scoticus*), black grouse (*Tetrao tetrix*), and capercaillie (*Tetrao urogallus*) in Scotland (Baines and Summers 1997), ptarmigan (*Lagopus lagopus*, *L. mutus*) in Norway (Bevanger and Brøseth 2000), and lesser prairie chicken (*Tympanuchus pallidicinctus*) in the United States (Robinson et al. 2016).

In some cases, fences erected deliberately to influence wildlife movements can help in the reduction of vehicle collisions with white-tailed deer (Falk et al. 1978, Bashore et al. 1985), or reduce crop damage (VerCauteren et al. 2006). Fencing has been used as a preventative measure for disease spread, including African swine fever in pigs (*Sus scrofa*; Dione et al. 2015), chronic wasting disease in reindeer (*Rangifer tarandus*; Mysterud and Rolandsen 2018), and foot-and-mouth disease in livestock (Dione et al. 2015, Jori and Etter 2016, Mogotsi et al. 2016). The goal of fencing for disease control is often to alter animal movement or to completely block

movements to reduce direct disease transmission. For example, the addition of electrical fencing near a pre-existing woven-wire fence reduced contact rates between farmed and wild elk (Fischer et al. 2011). Fencing does not completely eliminate the risk of transmission, due to contact rates of animals between fences, the ability for animals to pass through a single fence opening to allow disease transmission (Myserud and Rolandsen 2018), and spreading of the disease agent in the environment near the fence line (VerCauteren et al. 2007). Small animals that freely move through fencing, and human-caused animal movement of live or carcasses of animals also aid in disease transmission (Myserud and Rolandsen 2018).

The combination of fences with other anthropogenic features can magnify the barrier effect. For example, roads with fences on both sides are often significant barriers to animal movements, and can alter home ranges of wildlife (Ockenfels et al. 1997, Jaeger and Fahrig 2004). Fence placement can alter wildlife movement into high-risk areas, such as to funnel or entrap deer near interstate highways, which then face injury or mortality from vehicle collisions (Bellis and Graves 1971). Ungulates that attempt to jump over fences risk entanglement, usually with 1 or both hind feet, and subsequent injury or mortality (Harrington and Conover 2006). It is important for animals to be able to safely cross barriers, such as fencing, since animal populations benefit from connectivity (van Riper III and Ockenfels 1998). Some individuals or species are reluctant or incapable of jumping over fences and prefer to cross beneath fences (Harrington and Cover 2006, Burkholder et al. 2018).

Overall, fence type, height, and opening size beneath a fence influences the ease and method (jumping over or going underneath) by which different species will cross fences (Yoakum et al. 1980, Mackie 1981, Knight et al. 1997, Jones et al. 2017). Fence height often determines an animal's willingness to jump fences. For example, white-tailed deer may switch

their preference in jumping or passing underneath after modification of fence height and crossing height (Burkholder et al. 2018). Thompson (1978) found coyotes (*Canis latrans*) in captive conditions can climb 1.8-m fences, jump 1.5-m fences, and pass through 15.2 x 10.2-cm mesh fencing. Some species are more likely to cross under fences after modifications to existing fences, such as the addition of smooth (non-barbed) bottom wire or clips to elevate the bottom wire (Yoakum et al. 1980, Mackie 1981, Knight et al. 1997, Jones et al. 2017). Other species, such as pronghorn (*Antilocapra americana*), rarely jump fences, thus spacing of standard livestock fencing can strongly impede their movements (Yoakum 1980).

Since many animals prefer to dig or push under rather than jump fences, crossing sites are created from repeated crossing events. Crossings are recognized as sites where the bottom wire is pushed up or missing, often with a depression of bare soil with “runways” beneath (Fig. 3.1). Crossings are often created by animals that are strong enough to push up the bottom fence wire or dig beneath. For instance, feral swine (*Sus scrofa*) are known to create openings in fences (Bodenchuk 2010). Exotic wildlife, such as nilgai antelope (*Boselaphus tragocamelus*) also may contribute to the formation of fence crossings. The openings are then used by other wildlife species (Weise et al. 2014, Burkholder et al. 2018). Crossings are often found underneath net-wire livestock fencing on South Texas rangelands. Livestock fencing is common, but yet rarely studied for its’ impact on wildlife. As anthropogenic features are increasing worldwide, it is important to understand how fences impact movement of multiple species of wildlife. To gain information on animal impacts from fences, my objectives were to 1) assess fence crossing density, size, and location in South Texas, and 2) quantify animal usage of crossings.

STUDY AREA

I studied fence line ecology at 2 sites in South Texas, the East Foundation's East El Sauz and Santa Rosa Ranches (Fig. 3.2); both are maintained as native rangeland and working cattle ranches. The East Foundation is an Agricultural Research Organization that manages over 87,000 ha of rangeland across South Texas to promote the advancement of land stewardship through ranching, science, and education. Both sites have either 1.25-m or 2-m standard net-wire livestock boundary and interior fencing with 31 x 20-cm mesh to enclose cattle.

The East Foundation's El Sauz Ranch is 10,984 ha in size and borders the community of Port Mansfield, Willacy County, Texas (26°40'N, 97°35'W). The El Sauz Ranch is located in the Coastal Sand Plains, Lower Rio Grande Valley, and Laguna Madre Coastal Marshes ecoregions (Bailey et al. 1994). The Coastal Sand Plains contains active sand dunes, closed-depression ponds, and mid- to tall-grass prairie. The Lower Rio Grande Valley ecoregion is dense and diverse grassland, shrubland, and low woodland communities, with mostly Quaternary clay-loams and sandy clay-loam soils. The Laguna Madre Coastal Marshes are known for a hypersaline lagoon system, seagrass meadows, and tidal mud flats (Bailey et al. 1994). The characteristics from all 3 of these ecoregions are observed at El Sauz. Common vegetation communities include live oak (*Quercus virginiana*) woodlands, mesquite (*Prosopis glandulosa*) woodlands, gulf cordgrass (*Spartina spartinae*) grasslands, seacoast bluestem (*Schizachyrium scoparium* var. *littorale*) grassland, and marshhay cordgrass (*Spartina patens*) grassland. Port Mansfield had annual average precipitation of 64.3 cm and average mean temperature of 23.2°C during 1998–2018 (Prism 2018).

The East Foundation's Santa Rosa Ranch is 9,000 ha in size, located near the community of Riviera, Kenedy County, Texas (27°13'N, 97°51'W). The Santa Rosa Ranch is located in the

Coastal Sand Plain ecoregion (Bailey et al. 1994). Soils include Palobia loamy fine sand, Falfurrias-Cayo complex, Sarita, Nueces, and Sauz fine sand, and Yturria fine sandy loam (WSS 2018). Dominant vegetation communities include mesquite woodlands, huisache (*Acacia farnesiana*) woodlands, live oak woodlands, and spiny aster (*Leucosyris spinosa*) wetlands. Riviera had annual average precipitation of 70.7 cm and average mean temperature of 22.8°C during 1998–2018 (Prism 2018).

The East Foundation conducts annual aerial surveys for large mammals on each of their properties. These surveys involve flying transects via helicopter and using distance sampling (Thomas et al. 2002) to estimate population size for nilgai, white-tailed deer, feral swine, and collared peccary (*Pecari tajacu*). These surveys found nilgai and deer to be abundant on both the El Sauz and Santa Rosa sites. (East Foundation, unpublished data). For 2018 and 2019 surveys, respectively, estimates were 15 and 19 ha per deer at El Sauz, and 3 and 8 ha per deer at Santa Rosa. Nilgai estimates were similar between the sites, 9 and 6 ha per nilgai at El Sauz and 9 and 9 ha per nilgai at Santa Rosa. Feral swine and collared peccary were combined in these surveys, and El Sauz had 29 and 84 ha per feral swine and collared peccary, while Santa Rosa had 14 and 3 ha per feral swine and collared peccary.

METHODS

I drove alongside fence lines to verify the presence of intact, maintained boundary fences with little space between the bottom fence wire and the ground. I selected easily accessible fences that the only crossing options were from fence crossings created by animals. The fences selected were a 9,146 m boundary fence at El Sauz and a 2,174 m boundary fence at Santa Rosa. Both fences had 1.25-m tall standard net-wire livestock fences. Net-wire livestock fencing is common fencing in South Texas, and is perceived as durable with a long-lifespan (Isleib 1995). I drove a

utility vehicle along target fence lines at each site to record fence crossing locations, maximum bottom wire height (m) and width (m) of each crossing. When fence crossings become large, livestock can pass through, and a common practice is to repair the hole by securing a panel of livestock fence over the crossing (patch). I also recorded these patch locations to see their relation to fence crossing placement. I conducted fence crossing surveys in Fall 2017, 2018, and Spring 2018, 2019.

At each site, I randomly assigned 10 camera traps (Reconyx© HyperFire HC500 or XR6 UltraFire, Reconyx, Holmen, WI; Moultrie© A-5 Gen2 MCG-12688 Moultrie feeders, Alabaster, AL) to fence crossings identified through the fence surveys. I fastened cameras onto 5' metal t-posts at a mean height (\pm SE) above ground of 0.54 ± 0.02 m (range 0.43–0.63) at El Sauz, and 0.66 ± 0.03 m (range 0.40–0.80) at Santa Rosa. The mean distance (\pm SE) from the t-post to crossing was 3.00 ± 0.12 m (range 2.40–3.58) at El Sauz and 1.72 ± 0.15 m (range 1.04–2.80) at Santa Rosa. The boundary fence at Santa Rosa Ranch often had unpaved 2-track road close to the fence, restricting the distance between the crossing and the site of camera placement. Therefore, I placed the cameras higher up to angle down at the crossings. Cameras were first deployed in January 2018 as a pilot study to monitor the crossings and gauge quantity of photos, improve camera security, and placement. Cameras operated continuously and were checked every 2 weeks to adjust for any camera problems for the following 2 weeks. I programmed cameras to take a 3-photograph burst with a 10 s delay (Moultrie) or 15 s delay (Reconyx), with high motion detector sensitivity.

I classified the first 2 weeks (336 hours) of successful data each month per camera from April 2018–March 2019. I classified all animal events by species, time, date, and outcome of crossing event: successful or attempted crossing events, and animals captured on camera that did

not approach the crossing. Successful crossing events were defined as the 3-photo burst showing an animal passing through, or having at least half of the body through the fence crossing.

Attempted crossing events were classified as an animal's head making contact or close contact within the length of the fence crossing and either turned away or had no resulting photos of a successful cross. Animals in close proximity to the crossings, either between the camera and crossing, or on the opposite side of the fence that acknowledged (i.e., came in contact to look at, walk towards) the fence are also considered attempted events. Both successful and attempted crossing events were combined in the category "Crossing Events" (CE). Animals far off in the background of photos, or that clearly disregarded the fence (i.e. browsing nearby with photos of it walking out of the camera frame) were recorded but were not used in this analysis of fence line ecology. If I had consecutive photo bursts of clearly the same individual animal, it was not re-counted, unless it was present for >1 minute. I classified unrecognizable photographs of animals as unknowns, and in categories of unknown carnivore or unknown ungulate, when applicable.

To understand activity pattern of crossing events by multiple species, I categorized time into 8 parts of the day, each 3 hours, starting with 0500–0759 hr since 0500 hr best encompassed the time dawn or the first hour of light began during this study.

I calculated frequencies of crossing events per species, location, time, and season. I used SAS® software (SAS Institute Inc., Cary, NC) to compare the relationship between frequency of crossing events to fence crossing size. I used the Shannon-Weiner index to quantify species diversity and richness, excluding cattle, to account for both abundance and species evenness among sites (Shannon 1948).

RESULTS

I detected 34 crossings (1 crossing/269 m) and 30 patched crossings (1 patch/305 m) from Fall 2017–Spring 2019 at El Sauz. The El Sauz average crossing height (\pm SD) = 0.44 ± 0.13 m (range 0.18–1.00), width = 0.71 ± 0.26 m (range 0.21–1.70), and opening size = 0.32 ± 0.29 m² (range 0.06–1.09). Over half of the crossings (53%) were adjacent to previously patched crossings. At Santa Rosa, I detected 52 crossings (1 crossing/42 m) and 2 patched crossings (1 patch/1,087 m). One crossing was patched in December 2018, and the other patch was first recorded in the Fall 2018 survey next to a crossing. At Santa Rosa, the average crossing height (\pm SD) = 0.61 ± 0.13 m (range 0.31–0.94), width = 1.10 ± 0.44 m (range 0.33–3.00), and size = 0.69 ± 0.36 m² (range 0.15–2.6). For the 10 crossings monitored with cameras at El Sauz, the mean height (\pm SD) = 0.44 ± 0.09 m (range 0.32–0.60), width = 0.68 ± 0.11 m (range 52–93), and size = 0.30 ± 0.09 m² (range 0.18–0.43). The 10 crossings monitored at Santa Rosa had a mean height = 0.59 ± 0.11 m (range 0.35–0.73), width = 1.22 ± 0.33 m (0.79–1.67), size = 0.75 ± 2.91 m² (0.26–1.37).

Both sites had photographs of armadillo (*Dasypus novemcinctus*), bobcat (*Lynx rufus*), domestic cattle, coyote, white-tailed deer, feral swine, collared peccary, nilgai, raccoon (*Procyon lotor*), skunk (*Mephitis mephitis*), and turkey (*Meleagris gallopavo*). El Sauz also had an additional 4 species, including badger (*Taxidea taxus*), ocelot (*Leopardus pardalis*), lagomorphs (*Sylvilagus floridanus*, *Lepus californicus*), and other small mammals. Birds were classified but not used (besides turkey) in this analysis, since most were photographs of perching birds on the fence and other small birds that aren't dependent on crossing sites, such as roadrunners (*Geococcyx californianus*) and northern bobwhites (*Colinus virginianus*). Deer had the most crossing events at both sites (44% El Sauz, 58% Santa Rosa), followed by nilgai (14% El Sauz, 8% Santa Rosa; Fig. 3.3). Deer and feral swine successfully crossed at all fence crossings

monitored. Most crossings had success from collared peccary (95%), coyotes (90%), bobcats (67%), nilgai (71%), and raccoons (52%) at both sites.

The fence crossings at El Sauz had 6,229 CE with 50% success ($n = 3,128$), from 37,822 hours monitored (Table 3.1). At Santa Rosa, there were 4,660 CE with 67% success ($n = 3,143$), 35,763 hours (Table 3.1). Differences in monitoring hours were due to temporary camera malfunctions due to battery or other failure. El Sauz and Santa Rosa crossings, respectively, averaged 4.0 and 3.1 CE/day, and 2.0 and 2.1 successful events/day (Table 3.1). El Sauz crossing sites had CE ranging from 127 (1.1 CE/day) –1,289 (7.8 CE/day). Santa Rosa crossing sites had CE ranging from 260 (1.7 CE/day) –759 (5.2 CE/day).

I found a positive relationship between frequency of CE to size of fence crossing opening at both sites: El Sauz CE (d.f. = 9, $r^2 = 0.385$, $P = 0.056$ and Santa Rosa CE (d.f. = 10, $r^2 = 0.287$, $P = 0.089$; Fig. 3.5). Deer and swine successfully crossed at all unpatched fence crossings monitored. The smallest height recorded for deer success was 32 cm and the smallest size was 0.18 m². Nilgai successfully crossed at 7 of 10 crossings at El Sauz. The 3 crossings with no successful crosses from nilgai were 33–34 cm in height and 0.15–0.23 m². At Santa Rosa, nilgai successfully crossed at 8 of the 11 crossings monitored, the crossings nilgai did not use ranged from 35–52 cm in height and 0.26–0.80 m² in size. The smallest height for nilgai success at both sites was 44 cm and the smallest size was 0.26 m².

Species richness and diversity for El Sauz and Santa Rosa, respectively, was 14 vs. 10 species, and Shannon-Weiner index of diversity was 1.65 vs. 1.19. Overall daily activity patterns for CE were similar during morning, afternoon, and night, each contributing 21–30% of the total visitations (Fig. 3.6). Dawn consisted of the lowest percentage (9% for both sites), followed by dusk (13% El Sauz, 17% Santa Rosa; Fig. 3.6). At El Sauz, there were peaks in crossing activity

during May and between December–January for coyotes, deer, feral swine, collared peccary, nilgai, and turkey (Table 3.2). These species at Santa Rosa, besides feral swine, peaked from April–July and between December–February. Feral swine activity peaked in June and September at Santa Rosa (Table 3.2). Other species with <100 CE were excluded from this analysis, due to low occurrence.

During the pilot study, on March 28, 2018, two fence crossings were patched with a panel of livestock fencing at El Sauz. In response, I added cameras to 2 active, un-patched fence crossings, but also kept cameras at the 2 patched locations. These 2 patched crossings (ID: EF24 & EF25) provided an opportunity to assess wildlife response to a removal of well-established fence crossings. Both patched crossings were monitored from April 2018–March 2019. One of the patched crossings remained intact until August 3, 2018, when a nilgai bull pushed open the panel. This provided documentation of fence crossing re-establishment. A fence crossing at Santa Rosa was patched in December 2018, this camera was removed and placed on a new fence crossing to continue the evaluation of fence crossings use. Additional cameras were not available to investigate this patched location.

Patched EF24 had 285 CE/4 months from 8 species during April–July, and success from 1 bobcat and 5 turkey in May, and 2 coyotes and 3 collared peccaries in July. When opened, EF24 had 640 CE/8 months from 8 species during August–March. Successful CE occurred from coyotes, deer, feral swine, collared peccary, nilgai, raccoons, and turkey. Deer and nilgai were not recorded successfully crossing the 2 patched locations, heights both = 20 cm, and size = 0.14 m² and 0.20 m². I recorded deer and nilgai pushing their heads under the patch (Fig. 3.4), a bobcat and coyotes digging beneath the patch, and a bobcat climbing over the fence at the patch location. Average frequency of CE (CE/day) for EF24 was lower when patched (5.09, $n = 285$)

than when opened (6.53, $n = 640$). The frequency of successful crosses (events/day) was lower when patched (0.2, $n = 11$) than when opened (4.55, $n = 446$). Patched crossing EF25 remained intact throughout the study period from April 2018–March 2019. Crossing events occurred 237 times throughout the study from 9 species. Patched EF25 had success from 1 coyote and 4 feral swine in April, and 2 collared peccaries in March, and had 1.41 CE/day, $n = 237$. Before the crossing at Santa Rosa was patched, it had high use (4.4 CE/day, 490 CE) for the 8 months monitored, and was the largest crossing (1.37 m²).

Overall, successful CE roughly corresponded to population densities estimated through aerial surveys for nilgai and deer. Successful events/day for nilgai were similar between El Sauz (0.09, $n = 140$) and Santa Rosa (0.13, $n = 190$). White-tailed deer successfully crossed at Santa Rosa (1.43, $n = 2,143$) more often than at El Sauz (0.87, $n = 1,376$), similar to differences in population density. Feral swine had higher frequencies of successful crossing at El Sauz (0.36, $n = 566$) than Santa Rosa (0.166, $n = 248$), and collared peccary successful crossing frequencies were similar at El Sauz (0.12, $n = 183$) and Santa Rosa (0.17, $n = 249$).

DISCUSSION

Fence crossings clearly facilitate movement of wildlife in South Texas. In the absence of crossing sites, net-wire livestock fencing may act as a barrier to movement. Density and size of crossings varied by site and the overall age and condition of the fencing. Over half (53%) of the fence crossings at El Sauz were adjacent to patched locations, showing strong site fidelity for crossing locations. Crossing sites were used frequently by a diverse group of small and large wildlife. I found that 15 species of medium- and large-size mammals and birds used fence crossings, many of which may be less likely to cross otherwise. Both sites showed similar species and frequencies of wildlife using fence crossings, but overall, El Sauz had more crossing

events, species, and higher Shannon's diversity index than Santa Rosa. Both sites had similar percentage of successful crossings. Differences in CE but similar successful crosses, may be due to El Sauz having a newer fence in better condition than the Santa Rosa fence. The rate of crossing events I documented is staggering. The amount of successful crossing events alone exceeds any previous study of animal crossing use, especially since research on crossings underneath fences is limited and focused mainly on large mammals (Scott 1992, Weise et al. 2014, Burkholder et al. 2018).

Despite population estimates indicating higher densities of feral swine and collared peccary at Santa Rosa, overall successful fence crossing frequencies were higher for species at locations that showed higher density estimates. While many factors influence crossing rates, this indicates that fence crossing frequency could be related to animal densities.

Not all crossings were used equally; I found a positive relationship between crossing size and visits for both sites with much variation (Fig. 3.5). This finding is similar to other studies which found the number of crossing events increased for some species after modifications to existing fences, such as addition of smooth (non-barbed) bottom wire or clips to elevate the bottom wire (Yoakum et al. 1980, Mackie 1981, Knight et al. 1997, Jones et al. 2017, Burkholder et al. 2018). I found deer to successfully cross at ≥ 32 cm in height but not ≤ 20 cm, and with size ≥ 0.18 m². Nilgai did not successfully cross heights ≤ 35 cm or sizes ≤ 0.26 m². I did not find other species to be limited by fence height or size. To my knowledge, these are the first records of minimum heights and area required for white-tailed deer and nilgai to pass beneath fences.

Nilgai are the largest wildlife species that used these fence crossings, bulls $\bar{x} = 241$ kg vs. cows $\bar{x} = 169$ kg (Sheffield et al. 1983). Nilgai will fold in their front legs and tuck their head

under the crossing before pushing through, and there were often more than one photo-burst (10–15 s delay) of the same individual repeatedly trying to pass through the crossing, indicating hesitation. For deer and other animals, I typically had only one photo-burst of the animal crossing. Bauman et al. (1999) found white-tailed deer jump quickly over fences, having minimum contact with the fence. Although I did not quantify the amount of time it took animals to pass through crossings, I noticed that many of the deer and coyote photos were blurry since the animals moved quickly. Deer generally appeared to travel fast under the fence. I have observed deer and nilgai use fence crossings at full sprints at these sites as well. I did not identify individuals, but some animals were recognizable using the same crossings throughout the year (i.e., feral swine with distinctive spot patterns, or antlered bucks). Due to some individuals crossing repeatedly, the number of crossing events would be greater than the number of individuals that crossed.

Crossings were used at all parts of the day, and activity patterns were similar within-species between sites (Fig. 3.6). Armadillo, bobcat, coyote, feral swine, collared peccary, ocelot, raccoon, and skunk displayed nocturnal patterns (Fig. 3.6). Turkeys were diurnal, and cattle, deer and nilgai displayed crepuscular patterns (Fig. 3.6). These activity patterns are consistent with the species' behavior (Armadillo: Loughry & McDonough 2013; Bobcat: Chamberlain et al. 2003; Collared peccary: Ellisor and Harwell 1969; Coyote: Holzman et al. 1992; Feral swine: Campbell & Long 2010; Ocelot: Di Bitetti et al., 2006, Kolowski and Alonso 2010; Raccoon: Stuewer 1943, Ladine 2017; Skunk: Neiswenter et al. 2010; Deer: Michael 1970, Beier and McCullough 1990; and Nilgai: Singh et al. 2017). I observed crossing peaks during May and December–February for many species on both sites (Table 3.2). The peaks in winter may be attributed to rutting behavior of large mammals (Nilgai: Fall 1972, Sheffield et al. 1983; Deer:

Beier and McCullough 1990). In both cases, crossing activity corresponded with typical increase in daily and seasonal movements.

When crossings became vulnerable to cattle passage, landowners patched the fence crossings. To my knowledge, wildlife response to patched pre-established crossings has never been studied. While patching fence crossings is important to maintain fence integrity, wildlife often create new crossings adjacent to these patches. The 2 patches monitored clearly impeded deer and nilgai movements, and showed no successful crossing events. Patching did not limit all species. Bobcats, turkey, coyote, collared peccary, and feral swine successfully crossed the patched crossings (20 cm opening heights, and size = 0.14 m² and 0.20 m²). Animals still attempted to cross at these locations, with photographs of nilgai and deer pushing their heads under the patch, bobcats and coyotes digging beneath, and even a bobcat resorting to climbing over the patched fence after being unsuccessful at crossing beneath. These attempts to cross patched fencing often led to additional damage to the fence. Rather than constant fence maintenance, which is often a temporary fix, it may be helpful to create or reinforce fence modifications to prevent additional damage.

Most previous research on fence crossings only focused on single or few ungulate species, and excluded other animals in the analysis (Jakes et al. 2018). My study reveals the diversity of species that use fence crossings, showing the significant impact fences pose on animal movement. Previous research found net-wire fencing to be a strong barrier to pronghorn movement (Newman 1966, Bear 1969), white-tailed deer movement (Isleib 1995), and a source of grouse, ptarmigan, and prairie chicken collision mortality (Catt et al. 1994, Baines and Summers 1997, Bevanger and Brøseth 2000, and Robinson et al. 2016). Some fence designs have gaps near the ground (i.e., barbed wire or wooden rail) that are tall enough for small species

to cross without the need of pushing up or digging under the fence. It may not have been necessary for some previous studies to investigate all species that use crossings, since the fence may have only limited the large species, specifically ungulate species. With net-wire livestock fencing, I have photographs of bobcats and raccoons fitting through the 31 x 20 cm mesh, but they often still used crossings (Table 3.1). Thompson (1978) found coyotes in captive conditions can cross mesh as small as 15.2 x 10.2 cm, so coyotes should be able to cross through this fencing with ease. Larger animals, such as adult feral swine, nilgai, and deer, would be unable to fit through such a small area, hence the need to create or utilize existing crossings. Adult deer are capable of jumping these fence lines easily if desired. VerCauteren et al. (2010) found 0% deterrence rates for white-tailed deer with fence heights <1.5 m, and my fences were 1.25 m. Nilgai are capable of jumping fences but prefer to use fence crossings. During camera checks, some nilgai became alarmed and ran long distances along the fence, sometimes ramming their head into the fence to attempt to break through. Often, nilgai found a fence crossing or ran into the brush. I saw nilgai jumping a fence 3 times, with 1 resulting in the nilgai rolling as it hit the ground on the opposite side.

Surprisingly, there were numerous cattle CE ($n = 372$ and 615). While some cattle were only interested in rubbing the camera stakes, others investigated the crossings. It is important to understand livestock fence interactions in terms of contact rates between neighboring animals, both domestic and wild. The fence crossings monitored at both sites show visitation from both cattle and wildlife, which are locations to note for monitoring and controlling disease spread. Monitoring contact rates with fences has been a research interest in the case of several precautionary disease control measures, such as chronic wasting disease or bovine tuberculosis (VerCauteren et al. 2007, Lavelle et al. 2010, Fischer et al. 2011, Mysterud and Rolandsen

2018). Cattle are hosts for cattle fever ticks, and deer and nilgai are alternative hosts (Teel et al. 1996). I found these species to be primary users of fence crossings, revealing a high potential for disease transmission or spread between landholdings at crossing sites.

Net-wire livestock fencing is a common fence type used in South Texas, and I found maintained fences to be a barrier to wildlife movements. Many species are unable to cross net-wire fencing, leading to high use of fence crossings. Pre-existing crossings are sought out, and often re-established if patched. White-tailed deer were primary users of fence crossings, but 13 other wildlife species used crossings as well. These 2 sites in South Texas revealed the highest crossing rates, largest number of crossing events, and greatest number of species documented moving through fences, compared to previous research. While there is much variation in use among crossings, larger crossings often received more crossing events. About half of these attempted crossing events were successful.

These results provided contact and movement rates at fence crossings, which can be important to assess the potential for disease spread and to understand connectivity between landholdings. To my knowledge, this is the first fence crossing study conducted in South Texas, providing baseline information on movement rates and behavior associated with fence crossings as well as patched crossings.

MANAGEMENT IMPLICATIONS

Crossings in livestock fencing often result in damage to the fence, but are important for wildlife connectivity between landholdings. Patched crossings with additional wire fence are only a temporary solution to block the crossing, since many animals often ruin the patch or just damage the fence near it. Fence modifications, such as metal posts that limit the width size of a crossing or a horizontal metal bar at the desired fence crossing site size, may be a solution to reduce

damage over time and be a wildlife-friendly option for managers with net-wire livestock fencing. Crossings are known locations that last for long durations. Several wildlife species use fence crossing sites often, thus crossing sites could be targeted with disease control measures. There has been a recent interest in using crossing sites to administer cattle fever tick treatments to nilgai and white-tailed deer (Goolsby et al. 2019). The stability of these locations and frequency of visitations may be beneficial for disease control applications. Multiple species of wildlife, as well as domestic cattle, visit crossings frequently; therefore, crossings may pose high-risk areas for disease transmission between species and landholdings, or target locations to deliver pharmaceuticals to wildlife.

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Figure 3.1. Nilgai antelope bull passing beneath a net-wire livestock fence at an established crossing site on the East Foundation's El Sauz Ranch, June 2018. The back of the nilgai pushed up on the bottom wire and enlarged the crossing site, where repeated crossings by nilgai and other animals result in a recognizable opening and path under the fence.

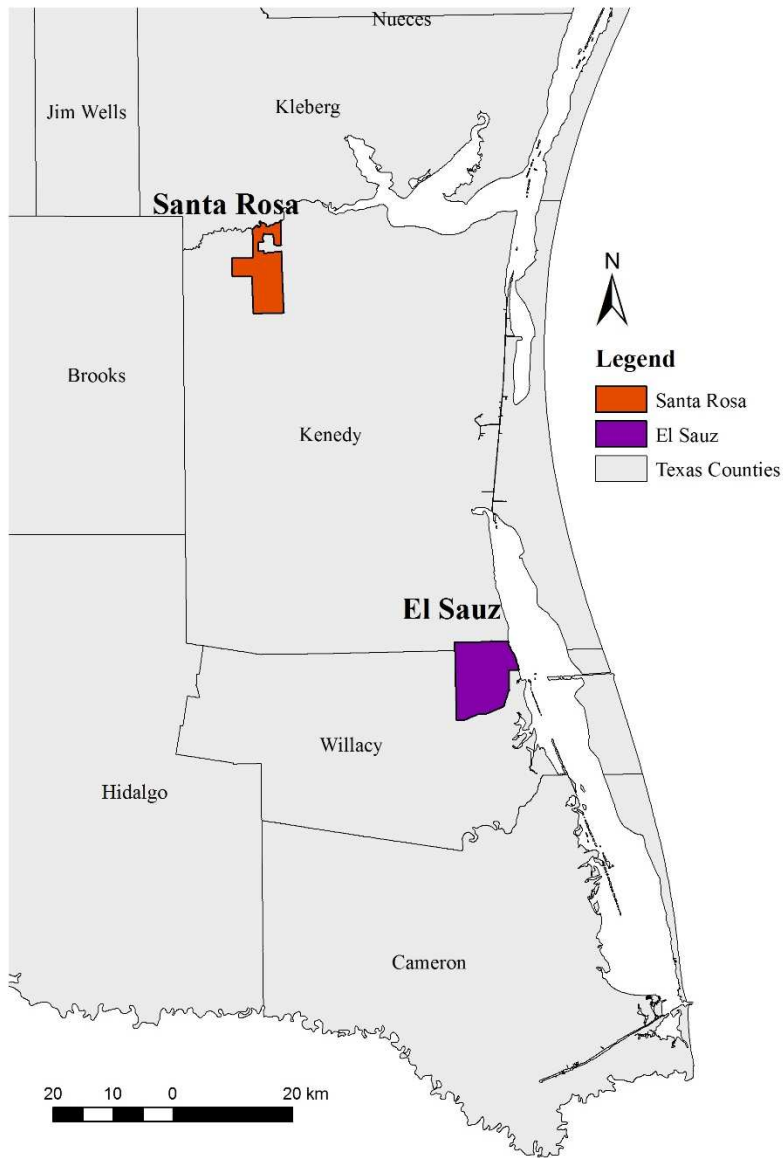
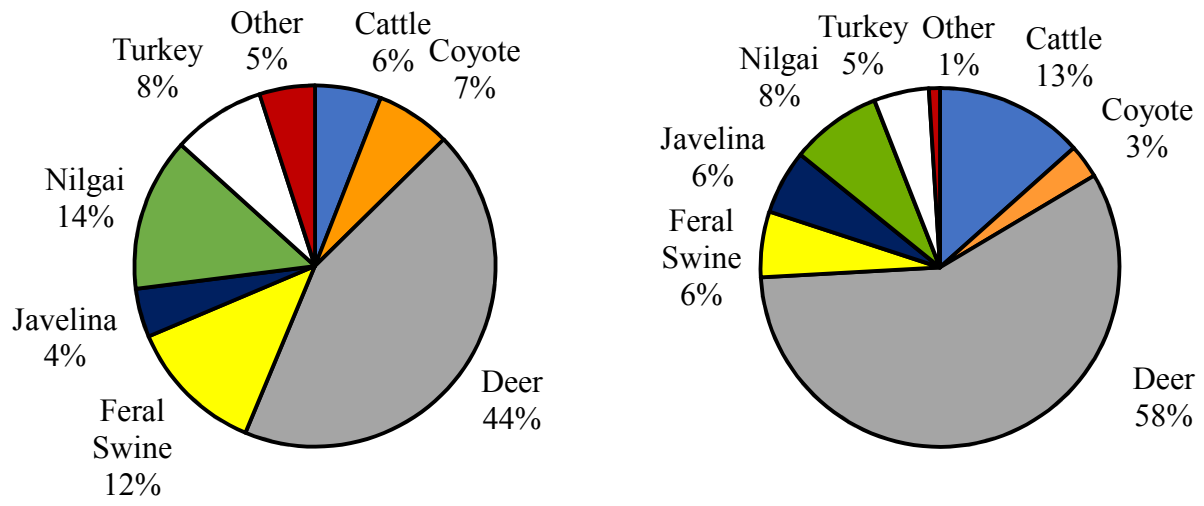


Figure 3.2. The East Foundation’s Santa Rosa and El Sauz Ranches in Kenedy and Willacy Counties, respectively, in South Texas. Camera traps were deployed on 10 randomly selected fence crossings at each ranch during April 2018–March 2019.



A

B

Figure 3.3. Species composition of fence crossing events at the East Foundation’s El Sauz Ranch (A) and Santa Rosa Ranch (B) in South Texas during April 2018–March 2019. Cameras were deployed at 10 randomly selected fence crossing sites at both El Sauz and Santa Rosa Ranches.



Figure 3.4. A nilgai antelope bull attempts to push through a patched crossing in a typical crossing stance at the East Foundation's El Sauz Ranch in South Texas, June 2018. When crossings become enlarged to the point of damage to the fence or allow livestock to escape, ranches repair and reinforce the fence. However, nilgai and other animals often persistently attempt to cross at the same site or nearby.

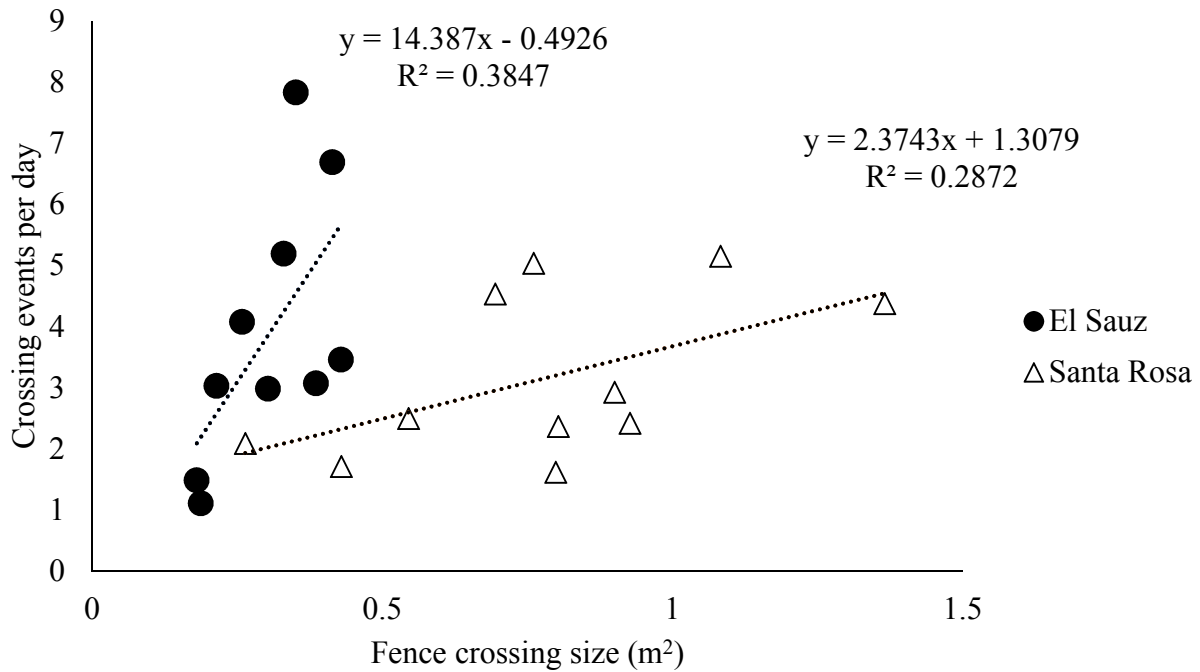
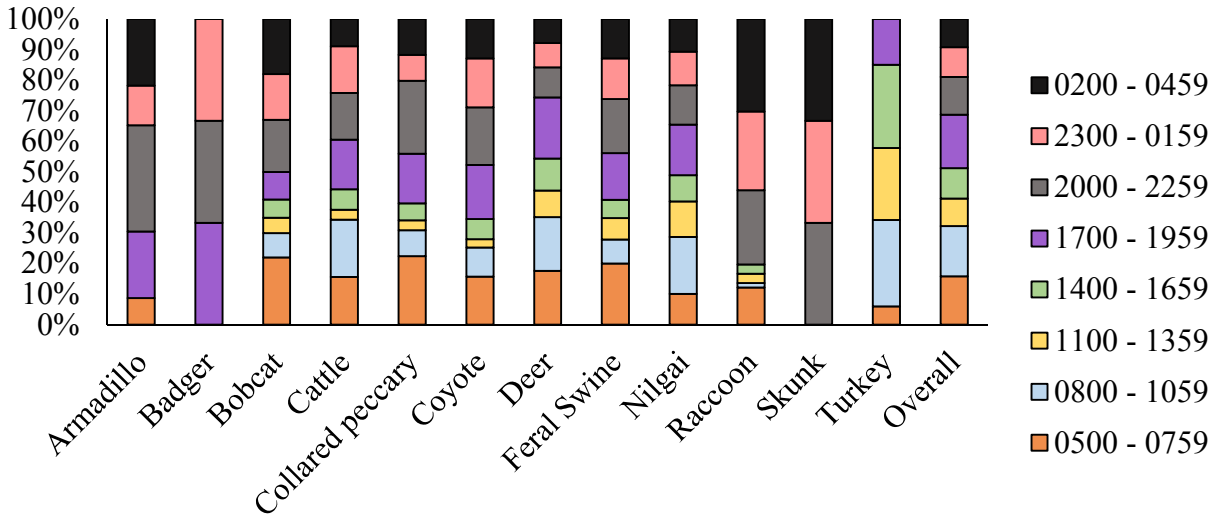
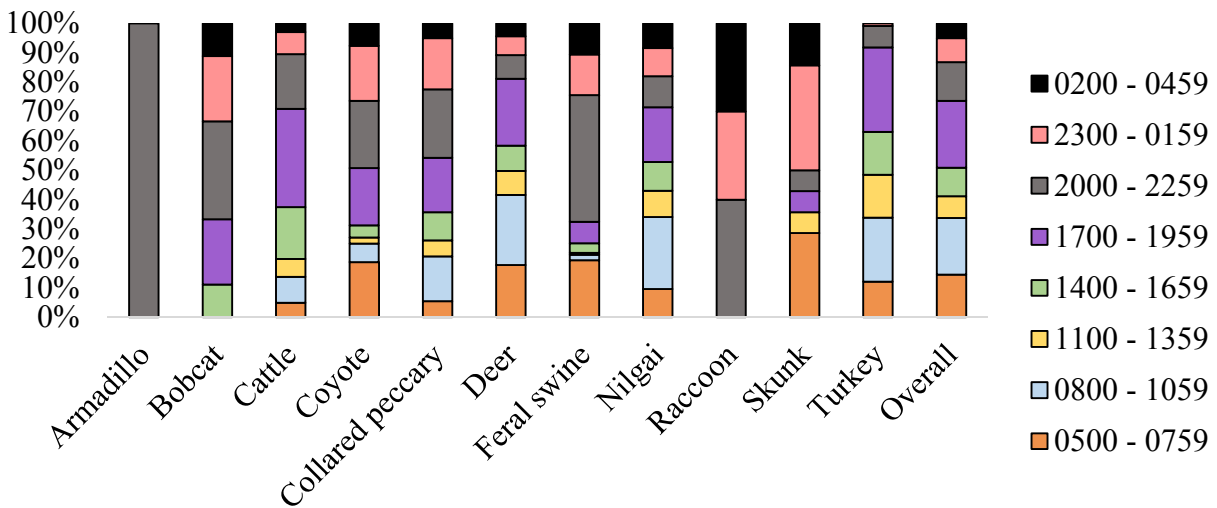


Figure 3.5. Average crossing events per day in relation size (m²) of the fence crossing sites on the East Foundation’s El Sauz and Santa Rosa Ranches, near Port Mansfield, Willacy County, and Riviera, Kenedy County, South Texas, respectively, during April 2018–March 2019. The crossing densities at Santa Rosa Ranch were greater (1 crossing per 42 m) than El Sauz Ranch (1 crossing per 269 m) due to the age and condition of fencing.



A



B

Figure 3.6. Daily activity patterns for species at fence crossing sites on the East Foundation’s El Sauz Ranch (A) and Santa Rosa Ranch (B) in South Texas during April 2018–March 2019.

Camera traps were deployed on 10 fence crossing sites at each ranch, where a site was defined as an area where the bottom fence wire was lifted or the ground was dug beneath the fence as a result of animals passing underneath the fence.

Table 3.1. Fence crossing events and frequencies by species during April 2018–March 2019.

Cameras were deployed at 10 fence crossing sites at each of 2 locations, the East Foundation’s El Sauz and Santa Rosa Ranches, in South Texas.

Species	Crossing events (successful ^a)		Avg. crossing events/day (successful ^a)	
	El Sauz	Santa Rosa	El Sauz	Santa Rosa
Armadillo	23 (15)	1 (1)	0.015 (0.010)	0.001 (0.001)
Badger	3 (3)	0 (0)	0.002 (0.002)	0.000 (0.000)
Bobcat	100 (88)	9 (9)	0.063 (0.056)	0.006 (0.006)
Cattle	372 (0)	615 (7)	0.236 (0.000)	0.413 (0.005)
Collared peccary	272 (183)	280 (249)	0.173 (0.116)	0.188 (0.167)
Coyote	419 (301)	144 (120)	0.266 (0.191)	0.097 (0.081)
Deer	2,738 (1,376)	2,690 (2,143)	1.737 (0.873)	1.805 (1.438)
Feral swine	776 (566)	274 (248)	0.492 (0.359)	0.184 (0.166)
Lagomorph	51 (13)	0 (0)	0.032 (0.008)	0.000 (0.000)
Nilgai	861 (140)	379 (190)	0.546 (0.089)	0.254 (0.128)
Ocelot	4 (3)	0 (0)	0.003 (0.002)	0.000 (0.004)
Raccoon	66 (42)	10 (6)	0.042 (0.027)	0.007 (0.008)

^aPhoto of an animal passing through fence crossing site or had at least half of the body through

Table 3.1. continued.

Species	Crossing events (successful ^a)		Avg. crossing events/day (successful ^a)	
	El Sauz	Santa Rosa	El Sauz	Santa Rosa
Skunk	3 (0)	14 (12)	0.002 (0.001)	0.009 (0.008)
Small mammal	1 (1)	0 (0)	0.001 (0.246)	0.000 (0.000)
Turkey	522 (388)	233 (155)	0.331 (0.005)	0.156 (0.104)
Unknown	14 (8)	7 (3)	0.009 (0.005)	0.005 (0.002)
Unknown carnivore	2 (1)	0 (0)	0.001 (0.001)	0.000 (0.000)
Unknown ungulate	2 (0)	4 (0)	0.001 (0.000)	0.003 (0.000)
Total	6,229 (3,128)	4,660 (3,143)	3.953 (1.985)	3.127 (2.109)

^aPhoto of an animal passing through fence crossing site or had at least half of the body through

Table 3.2. Peak months in fence crossing events for species with > 100 events on the East Foundation’s El Sauz and Santa Rosa Ranches in South Texas from April 2018–March 2019.

Data were collected from camera traps deployed at 10 fence crossing sites at each ranch.

Species	Peak months			
	El Sauz		Santa Rosa	
Bobcat	Dec	NA	NA	NA
Collared peccary	May	Jul	Jul	Dec
Coyote	Jan	May	Jun	Apr
Deer	Jun	Jan	Dec	Jun
Feral Swine	May	Jan	Jun	Sep
Nilgai	May	Jan	Jun	Feb
Turkey	May	Mar	Apr	Jun

CHAPTER IV

IMPLICATIONS FOR THE ERADICATION OF CATTLE FEVER TICKS

Background

There is a special interest and acceptance in Texas for exotic ungulates in ranching and hunting, but little is known about the ecology and behavior of many exotics (Ables and Ramsey 1972). Despite over 80 years since the introduction of nilgai antelope (*Boselaphus tragocamelus*) to South Texas (Leslie 2008), basic ecological research on nilgai is lacking in both Texas and their native range in India, Nepal (Dinerstein 1980), and Pakistan (Mirza and Khan 1975). Nilgai present an important management challenge due to their potential role in the transmission of cattle fever ticks (CFT; *Rhipicephalus microplus*) in South Texas. Cattle fever ticks (*Rhipicephalus annulatus* and *R. microplus*) are vectors for the protozoan parasite *Babesia bovis* (= *B. argentina*; *B. Berbera*; *B. colchica* and *B. bigemina*) in the larval stage (Mahoney and Mirre 1979, Teel et al. 1996). These protozoans cause bovine babesiosis, also known as “Texas Fever” or “Cattle Fever,” in cattle worldwide (Bock et al. 2004). Clinical symptoms include high fever, depression, increased respiration, hemoglobinuria, decreased movement (Bock et al. 2004), abortion of fetuses (Callow 1984), and coma (de Vos and Potgieter 1994). Infected cattle can remain as asymptomatic carriers for months after recovery from clinical symptoms (Mahoney 1969, Johnston et al. 1978).

Cattle fever ticks once infested most of the southeastern U.S., but through a cooperative state–federal program, the U.S. began eradication of CFT in 1907 and completed eradication in 1960 (Graham and Hourrigan 1977). Eradication measures involved either dipping livestock in an acaricide every 7–14 days to disrupt the tick life cycle, or vacating cattle from premises for nine months (Graham and Hourrigan 1977, TAHC 2017). Cattle fever ticks are one-host ticks,

and removal of their host (cattle) interrupts infestation. The program was successful, and bovine babesiosis and CFT were eradicated from the U.S. The 1906 estimated direct and indirect economic loss *R. annulatus* and babesiosis had on the U.S. was \$130.5 million annually, equivalent to over \$3.6 billion in today's currency (James and Harwood 1969).

The U.S. is still threatened by CFT because of occasional re-emergence of CFT along the southern border from Mexico, where the ticks are endemic (Graham and Hourrigan 1977). Incursions of CFT into South Texas from Mexico required the establishment of permanent and temporary quarantine zones to monitor cattle and wildlife (TAHC 2017). The permanent eradication quarantine area for CFT between Texas and Mexico is about 183 m–1.6 km wide along the Rio Grande River bordering 8 counties (Fig. 4.1). In all quarantine areas, cattle, horses, and other livestock cannot be moved until inspection and treatment for ticks. A written permit or certificate from a Texas Animal Health Commission representative is required for movement of animals within this area. If CFT are found on any animal on a property, it is classified as an “infested premises.” Ticks are managed via chemical treatments or physical separation from the host. Both approaches can be burdensome for landowners. Livestock are sprayed or immersed into acaricide solution every 1–2 weeks for 6–9 months, or administered injectable or oral parasite medications (i.e., Ivermectin in molasses tubs) given at 25–28 day cycles during the quarantine period. Removal of livestock from the premises for 9 months is an alternative to chemical treatments (TAHC 2017). After 2 CFT-free inspections, cattle can be transported on or off a property (TAHC 2017). While tick treatments are difficult on domestic animals, wildlife pose a greater challenge to treat and control from spreading CFT. White-tailed deer and nilgai antelope are alternative hosts for CFT (Teel et al. 1996). Control methods, such as treated baits, are available for deer. However, nilgai are not habituated to consume bait, and nilgai are also

wary in nature, a major challenge for controlling the spread of CFT. Nilgai are considered an exotic animal by the Texas Parks and Wildlife Department, and there is no restriction on harvest. Year-round harvest of nilgai raises a concern if medicated bait is distributed, since there needs to be a withdrawal time before meat can be safely consumed. For white-tailed deer, there is a 60-day withdrawal time before harvest, allowing the elimination of Ivermectin residue before human consumption (USDA APHIS 2016). This raises a problem in how to safely deliver chemical treatments to nilgai. The only current management of CFT in nilgai is through construction of game-proof fencing to limit the spread of ticks, or to reduce the density of nilgai via harvest. Neither alternative is palatable, as game-proof fencing is cost-prohibitive, and nilgai have an economic and recreational value to landowners. Despite efforts to reduce nilgai populations in some areas, nilgai quickly re-populate because of their ability to move long distances (Foley et al. 2017). Furthermore, nilgai have a high reproductive rate, often giving birth to twins (Fall 1972, Sheffield et al. 1983, Bagchi et al. 2008).

Recently, managers proposed the strategy of topical application of acaricides via remotely activated sprayers for tick treatment of nilgai (Goosby et al. 2019). These sprayers have the potential to deliver a non-toxic native nematode (*Steinernema riobrave*) that could kill CFT on target animals with no withdrawal or toxicity issues (Goosby et al. 2018, 2019, Singh et al. 2018a, b). The challenge is how to attract nilgai to the sprayer sites. The sprayers need to be placed in areas frequently visited by nilgai. To implement an efficient CFT eradication measure on nilgai, further information on nilgai movement and behavior ecology is needed. Nilgai latrines and fence crossings are fixed areas that nilgai repeatedly re-visit. There has never been a study on nilgai latrine or fence crossings use to assess if these locations would be useful areas to

place treatment measures. My goal was to investigate the potential of latrine sites and fence crossings for delivery of CFT treatments to nilgai.

Nilgai antelope latrines

Nilgai latrines were abundant in all vegetation communities, with site-specific estimates of 244–10,206 latrines. Latrines were more abundant on unpaved roads than off-roads, but it would not be feasible to place treatments on all latrines and especially ones inaccessible from roads. About 40% of the latrines surveyed on unpaved roads were only detected for 1 survey period, or <6 months. Also, latrine densities were greater than nilgai population estimates, indicating nilgai must use multiple latrines.

Nilgai visited latrines at low frequencies, about once every 2–3 days. Defecations averaged 1 event per 12 days. Latrines were visited mainly by bulls (70%), and most (94%) defecations were from adult bulls. Latrines had similar peaks in activity to fence crossings during spring and winter. Latrines were more abundant and larger in spring, following the peak in the nilgai breeding season. While it would be beneficial to target treatments during times of high visitation rates (winter), there could be a higher abundance of latrines during that time. Latrine function appears related to territorial display, and defecation rates could be driven by latrine location relative to neighboring territorial bulls or intruder defecations (Brashares and Arcese 1999, Black-Decima and Santana 2011), location of territory boundaries (Kruuk 1978, Brashares and Arcese 1999), or cow defecation-urination to display reproductive receptivity (Roberts and Dunbar 2000). It would be difficult to determine which latrines would get higher visitations than others, and frequency of visitations changed often, which makes selection of high-use latrines for treatments challenging.

I identified 16 species of non-target animals that visited latrines, animals that could be affected by a tick treatment deployed at latrine sites. Nilgai only contributed to 15% of the latrine visits, but deer, cattle, and nilgai combined contributed to >70% of the visits for each of the 3 sites surveyed. Nearly half of the nilgai that visited a latrine stepped on the latrine, thus a greater chance that a nilgai visiting could be directly sprayed. Both photos and genetic data indicated repeated visitations from the same individuals, mostly adult bulls. Nilgai of all age and sex classes can carry cattle fever ticks, and administration of a treatment is ideal for all cohorts. The original assumption that many nilgai use the same latrine is not accurate; while multiple nilgai may visit latrines, most visits and defecations are from the same individual.

Fence crossings

Not all South Texas ranches with nilgai have net-wire livestock fences, but for sites that do, the density of fence crossings is variable depending on the amount of fence maintenance and animal movements. I found that crossings within livestock fencing tend to persist in the same locations. Even after a crossing was patched, new crossings often became established adjacent to fence patches. Crossings are easily found, defined, stationary locations, which is beneficial for implementation of a system for tick treatment measures. Nilgai visited crossings at low frequencies, about every 2–3 days. Crossings were used by all sex and age classes of nilgai, with 46% bulls, 44% cows, and 10% calves or unknowns. Crossing events peaked in spring (around May) and winter (December–February) for most species, including nilgai. This corresponds to a peak in the nilgai breeding season during December–March (Fall 1972, Sheffield et al. 1983). December–February would be an optimum time to treat nilgai more frequently, but there was increased use by other wildlife species at that time as well.

I recorded 15 animal species that attempted or successfully crossed at a fence crossing site. On average, 3–4 crossing events from animals occur each day at a given crossing, but visitations were variable among locations. Nilgai contributed to only 11% of the fence crossing visits. When examining all hosts of cattle fever tick (cattle, nilgai, and deer), combined they contributed to most of the crossing events, 64% and 79% at the East Foundation's El Sauz and Santa Rosa Ranches, respectively. About half of the crossing events, 50% (El Sauz) and 67% (Santa Rosa), were successful. Crossing frequency was variable among locations, but typically larger crossings received higher visitation rates. Crossing size did not limit most animals other than nilgai and deer. Nilgai did not successfully cross fences where the bottom fence wire was ≤ 35 cm above the ground, or sizes ≤ 0.26 m², and deer successfully crossed at ≥ 32 cm in height but not ≤ 20 cm, or < 0.18 m². Managers should focus on crossings > 35 cm in height for treatments for nilgai.

If sprayers were implemented on crossings for nilgai and we assume these crossings are comparable to crossings with sprayers operating at 100% efficiency, I estimated a low percentage of triggers, 14% (El Sauz) and 8% (Santa Rosa) would be targeted on nilgai. I estimated only 2% of the total triggers at El Sauz and 4% at Santa Rosa would be on nilgai that successfully cross through the fence. Foley et al. (2017) found 1,051 nilgai fence crossing approaches to boundary fences from April 2015–June 2016, with 0.15 fence crosses per approach by nilgai at El Sauz boundary fences. This indicates not all fence approaches result in a successful cross thus, the spray area must be large around the crossings to target nilgai that do not commit to successfully crossing the fence. At these sites, a sprayer could be activated about 3–4 times a day by an animal, and could be triggered any hour of the day, especially for nilgai. This is important to note, to estimate the potential volume of treatment solution used per day, and

how frequent a sprayer needs to be replenished. I recorded 15 species that could potentially be treated. Thus, this emphasizes the necessity for safe treatments for all animal species, such as the proposed entomopathogenic nematode solution fits this requirement (Goolsby et al. 2018, 2019, Singh et al. 2018a, 2018b). Sensitivity or height of a sprayer sensor should be adjusted to reduce triggers from small animals to reserve treatment for large animals, such as nilgai and white-tailed deer.

My results do not indicate the number of individual animals that cross fences, so the number of crossing events from the same individuals were unknown. Having the same individual targeted multiple times would help with a continuous re-application of treatments, but there is a greater need for a large-scale treatment of individual nilgai. Further research must be done to understand the reaction of animals to a spraying device, the efficiency of the treatment application, and the number of individual nilgai that could be affected.

Overall, crossing sites could be useful for placement of treatment measures since crossings are stationary, visited by all sex and age classes of nilgai, and most visitations are from CFT hosts (cattle, deer, and nilgai). Focused efforts should be on larger crossings and ones >35 cm in height and >0.26 m². Determination of the proportion of the same nilgai individuals that visit crossings would help managers better understand the efficiency of crossings sites for tick treatments.

Conclusions

Since there is limited information on nilgai antelope, continued research on basic nilgai ecology is needed to help the cattle fever tick eradication program establish treatments for CFT on nilgai. This study provides information that is valuable to show latrine sites as unfeasible locations for tick treatments, and inefficient with target to mainly adult bulls. It would also be a burden to

move sprayer treatments frequently. Results indicate fence crossings are more promising locations for administration of tick treatments. Research on the number of individual nilgai that use crossings, and sprayer efficiency is needed to further enhance efficiency of a nilgai tick control measure. The results of this study have important implications for the development of treatment methods on nilgai, for eradication of CFT in the U.S.

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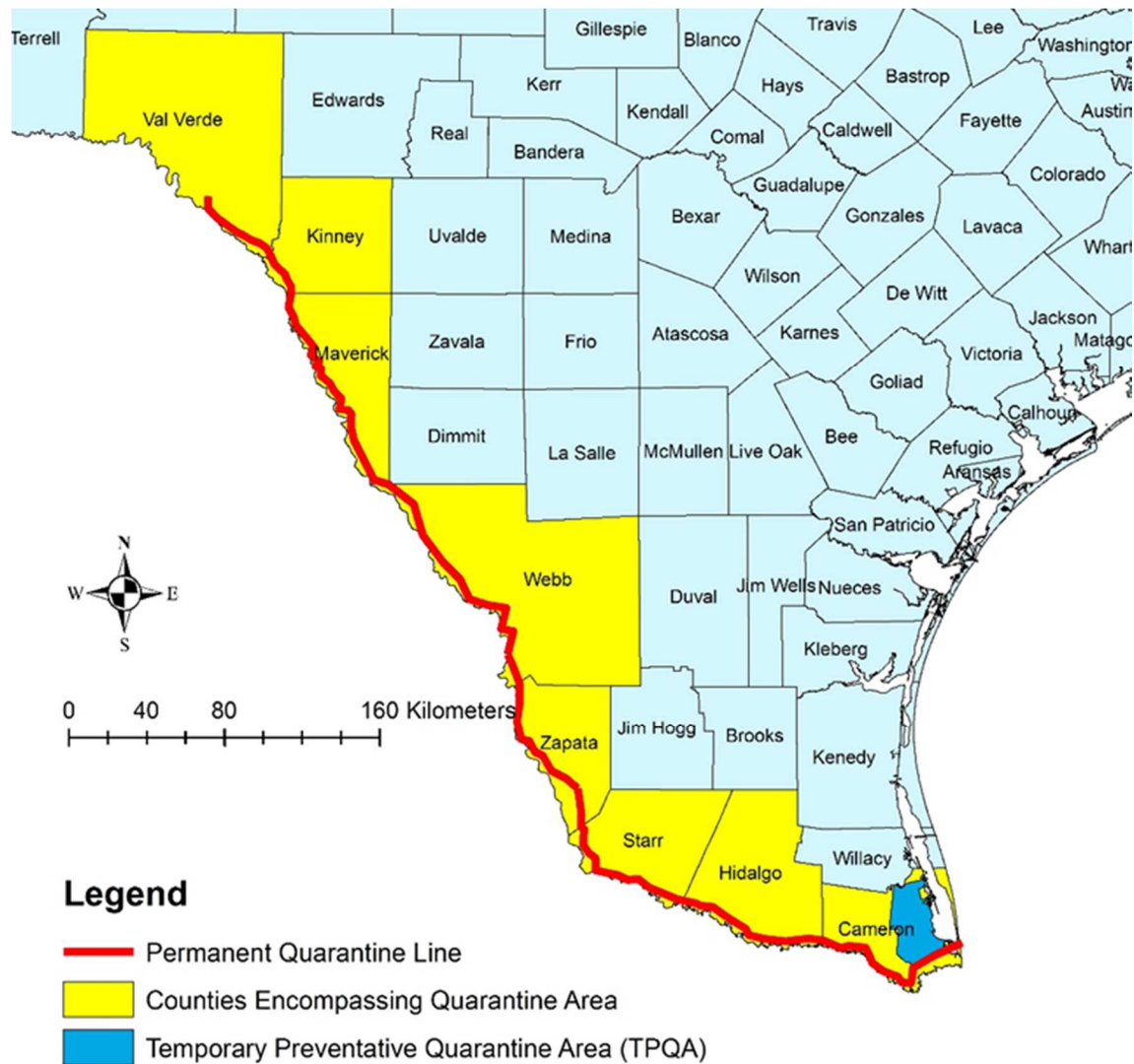


Figure 4.1. The Cattle Fever Tick Eradication Program maintains a permanent quarantine line (2019) along the Rio Grande river in Texas, to quickly respond to intrusions of cattle fever ticks (CFT) of stray cattle along the Mexico border. The Temporary Preventative Quarantine Area in eastern Cameron County was created due to infestations of CFT inland, requiring landowners to eradicate CFT (TAHC 2017).

VITA

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- 3-MT Speaking competition finalist 2018
- Barrientos Academic Scholarship (\$1,300/semester) 2017–2019
- The Aldo Leopold Undergraduate Scholarship Award (\$1,000) 2017
- North Central Section Wildlife Undergraduate Student of the Year Award (\$500) 2017
- Wilson CNR Outstanding Undergraduate Student Scholarship (\$1,500) 2017
- UWSP Albertson Medallion Award 2017
- UWSP Chancellor's Leadership Award 2017
- Martha E. Sorensen Outstanding Junior of CNR Scholarship (\$1,250) 2016
- Undergraduate Student Poster Honorable Mention-Nat. Wildlife Society Conf. 2016
- Marv and Sandy Kramer Summer Academic Scholarship (\$1,000) 2015