Articles

Density of Axis Deer in Texas: Management Implications for Native White-tailed Deer and Associated Habitats

Matthew J. Buchholz,* Warren C. Conway, Thomas L. Arsuffi, Mitch L. Lockwood, Blake A. Grisham

M.J. Buchholz, W.C. Conway, B.A. Grisham
Department of Natural Resources Management, Texas Tech University, Lubbock, Texas 79409

T.L. Arsuffi
Llano River Field Station, Texas Tech University, Junction, Texas 76849

M.L. Lockwood
Texas Parks and Wildlife Department, Kerrville, Texas 78028

Abstract

Axis deer *Axis axis* have been widely introduced to new geographic ranges, and in the United States, free-ranging axis deer have become well established in the Edwards Plateau ecoregion as well as other portions of Texas. However, no estimates of axis deer population density nor size have been conducted since 1994. It is hypothesized that axis deer on the Edwards Plateau are potentially competing with native white-tailed deer *Odocoileus virginianus* for food, space, and habitat resources, and causing damage to important riparian habitats. Our goal was to estimate regional densities of axis deer and white-tailed deer, and provide insight about the potential impacts axis deer may have on native wildlife and their habitats. Estimated using distance sampling techniques in 2018 and 2019, average axis deer density was 19.7 (95% CI: 14.1–25.6) axis deer/km^2 compared with 23.0 (95% CI: 18.2–27.5) white-tailed deer/km^2, and axis deer densities ranged from 16.9 to 171.0/km^2 among eight different land cover types in Kimble County, Texas, with a county-wide estimate of 61,078 (95% CI: 30,407–100,369) axis deer. Axis deer densities were greatest in riparian land cover types, and they selected for two riparian land cover types and upland grasslands. Axis deer population estimates clearly indicate their population size has increased substantially since introduction to Texas in the 1930s. Population management of axis deer is warranted to limit impacts to native wildlife from potential habitat usurpation, or damage to riparian vegetation communities, soil, and water quality.

Keywords: *Axis axis*; axis deer; Edwards Plateau; introduced species

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* Corresponding author: matthew.buchholz588@gmail.com

Introduction

The axis deer *Axis axis* is a cervid native to the Indian subcontinent (Randall and Tomeček 2021) that have been widely, and intentionally introduced to new geographic ranges during the 19th and 20th centuries including into North and South America, Oceania, and Europe (Graf and Nichols 1966; Ables 1977; Moriarty 2004; Novillo and Ojeda 2008; Kusak and Krapinec 2010). Axis deer have been ranked as the 31st worst invasive alien plant or animal species in Europe via a standardized scoring system that assessed ecological and socio-economic impacts (Nentwig et al. 2018). In the United States, free-ranging axis deer are common in the

Edwards Plateau ecoregion (EPE; Gould et al. 2011) of Central Texas, which is considered to have the greatest density, abundance, and potential negative impacts by axis deer (as well as the greatest density and abundance of white-tailed deer *Odocoileus virginianus* in Texas) throughout their introduced range within North America (Ables 1977; Broad et al. 2016; Schmidly and Bradley 2016; Cain 2020; TPWD 2021a). Environmental similarities of the EPE to native ranges of axis deer in India have provided some of the requisite conditions for axis deer to thrive in their introduced range in Texas (Ables 1977).

Axis deer initially were initially introduced to captive high-fenced ranches in Texas in 1932 to provide hunting opportunities, but have since formed free-ranging herds throughout the EPE (Mungall and Sheffield 1994; Gould et al. 2011; Schmidly and Bradley 2016; TPWD 2021b) and other portions of Texas. Anecdotal estimates of axis deer population size (both free-range and captive) in Texas were obtained approximately every 5 y from 1966 to 1994 by the Texas Parks and Wildlife Department (TPWD; Traweek 1995). The total statewide population was estimated to be only 6,450 individuals in 1966, and the most recent population estimate conducted in 1994 reported ~23,000 free-ranging axis deer, with an additional ~29,000 on high-fence ranches for a total of ~52,000 individuals occurring in 100 of 254 Texas counties (Traweek 1995). Most free-ranging axis deer were recorded in Kerr, Kimble, and Real counties in the EPE (6,000, 5,000, and 4,000 respectively; Traweek 1995). Together, these older reports clearly indicate significant growth in axis deer regionally during that ~30-y time period, where the Kerr County 1994 estimate was nearly equal to the statewide estimate in 1966. However, no other additional regional nor statewide surveys have been performed since that we are aware of, and the current abundance of axis deer, particularly those that are free-ranging in Texas, remains unknown.

Based on field observations and other anecdotal reports from landowners and local biologists, axis deer in the EPE are increasing in both abundance and localized densities, and are expanding their geographic distribution regionally. Combined, these factors have provided the conceptual foundation for concerns regarding their potential competition with native white-tailed deer for food, space, and habitat resources, and their regional impact on riparian habitats (Broad et al. 2016). Both axis deer and white-tailed deer are sympatric at multiple spatial scales (home range, core areas, food sources) regionally, where axis deer often occupy more open habitat compared with white-tailed deer, but also use stands of dense cover that white-tailed deer typically occupy (Elliott and Barrett 1985; Henke et al. 1988; Mungall and Sheffield 1994; Demarais et al. 1998, 2000; Faas and Weckerly 2010). Although axis deer diets consist of more grass than do white-tailed deer diets, axis deer possess a broader diet breadth and will also consume browse, mast, and forbs that constitute the bulk of white-tailed deer diets in the ecoregion (Ables 1977; Elliott and Barrett 1985; Henke et al. 1988). The advantage of this wide diet breadth may be amplified by the increase in magnitude and frequency of droughts that decreases food availability for white-tailed deer (Folks et al. 2014). During periods of drought (and other times where shared resources are limited), axis deer may shift their diet to grasses (Butts et al. 1982), which may facilitate some competitive advantage(s) over white-tailed deer that may struggle to find sufficient food resources during these times. More specifically, axis deer "win" during episodes of food-centric interspecific and interference competition with white-tailed deer, with whom they are socially dominant (Faas and Weckerly 2010). Axis deer consistently displace white-tailed deer from foraging locations and white-tailed deer tend to shift habitat use in the presence of axis deer (Faas and Weckerly 2010).

Axis deer are associated with riparian habitats (sensu Hall et al. 1997) in India and Texas, particularly riparian grasslands (Moe and Wegge 1994; Bhat and Rawat 1995; Sharma and Chalise 2014). However, they will use a diversity of land cover types, ranging from mixed grasses and shrubs in Sri Lanka, to dense forests in India (Eisenberg and Lockhart 1972; Berwick 1974), to semi-deserts and rainforests in Hawaii (Graf and Nichols 1966). Their propensity to occur in a wide diversity of land cover types may facilitate their ability to persist and affect their new ecosystems. For instance, axis deer are suspected to contribute to bacterial and nutritional loading of streams (Broad et al. 2016) via their propensity to use the same trails daily, potentially contributing to erosion and compaction of riparian soils (Schaller 1967; Zuazo and Pleguezuelo 2008). Previous research has advanced the notion of the negative effects of abundant axis deer and white-tailed deer in Texas on soil and vegetation communities. For example, Ables (1977) reported that certain forb species had greater density, grass cover was almost three times as great, and plateau live oak *Quercus fusiformis* seedlings were substantially taller inside deer-proof exclosures that excluded both axis deer and white-tailed deer. The cumulative effects of herbivory by axis deer and white-tailed deer, coupled with increases in axis deer abundance and density regionally, have provided the foundation for more specific studies examining their impact on riparian zones for the ecologically important rivers in the EPE (Broad et al. 2016).

To address potential management concerns regarding increasing axis deer abundance in portions of Texas and potential negative impacts on native white-tailed deer and habitats, we had several objectives for this research. Specifically, this work focused upon estimating relative densities of axis deer and white-tailed deer including temporal variation in the density of both species, proportional habitat use by axis deer, and axis deer population growth. First, we conducted line-transect surveys to estimate and compare axis deer and white-tailed deer density in Kimble County, Texas, 2018–2019 because density and abundance data (both species-specific and combined) are critical to understanding potential ecological impacts and assess future management goals. Second, we sought to assess densities of axis deer and white-tailed deer temporally to examine potential seasonal and other abiotic factor impacts on density. Third, we estimated axis deer densities in

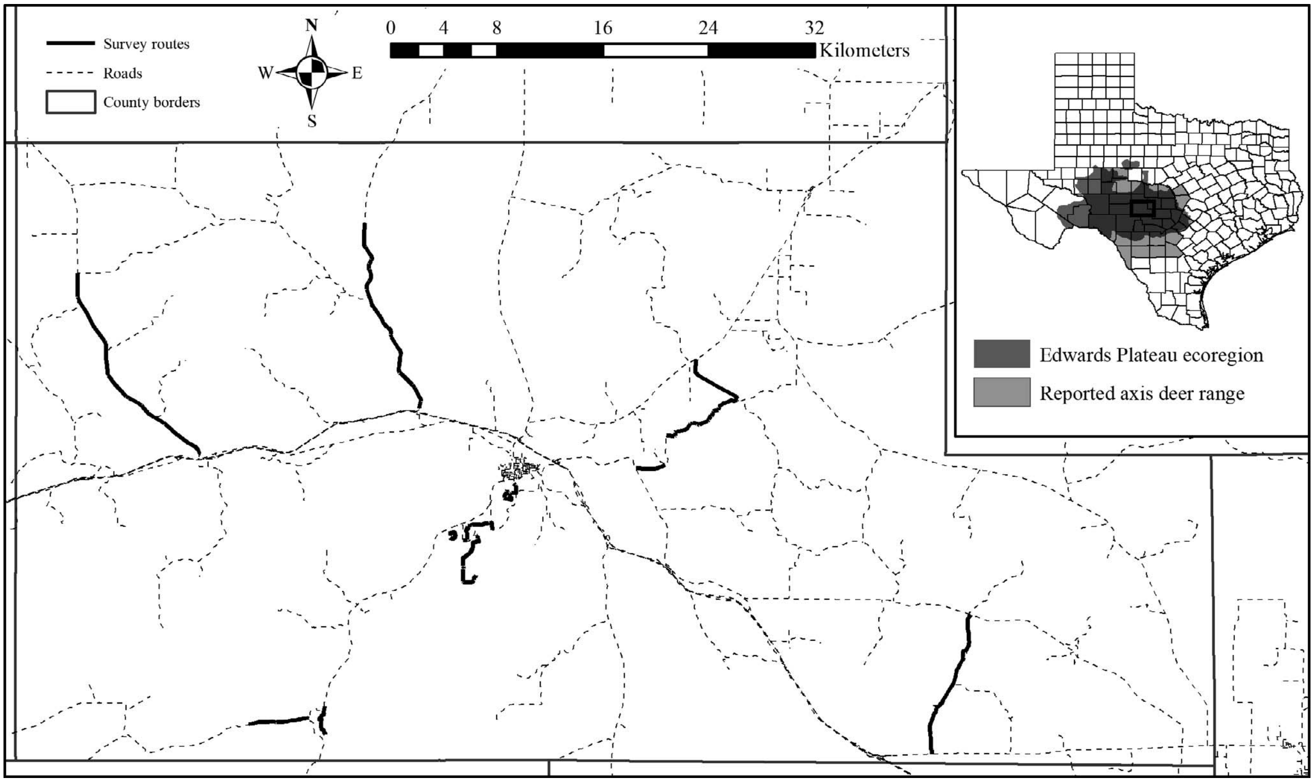

Figure 1. Spotlight survey routes used for distance sampling of axis deer *Axis axis* and white-tailed deer *Odocoileus virginianus* in Kimble County, Texas, 2018–2019 in the Edwards Plateau ecoregion (EPE) and reported county-level distribution of free-range axis deer in Texas.

different land cover types in Kimble County to assess whether, and where, they may be having disproportionate ecological impacts. We then used these density data to develop habitat selection indices for axis deer among land cover types, in a "used vs. available" selection framework. Finally, we estimated axis deer population size for Kimble County for all land cover types combined to assess population growth rate and obtain the first empirical estimate of axis deer abundance anywhere in Texas.

Study Site

Kimble County

We conducted this study in Kimble County, Texas (30.5°N, 99.7°W), in the EPE of Texas (Figure 1; Gould et al. 2011). Kimble County, Texas, consists almost entirely of portions of the Upper Llano River Watershed, comprising the tributaries and drainages of the North and South Llano rivers and the Llano River Watershed, which consists of the Llano River and its tributaries after the North and South Llano rivers converge in Junction, Texas (Figure 1). An Upper Llano River Watershed protection plan has recently been completed, with the mission to inform and direct research and conservation approaches for the watershed (Broad et al. 2016). The South Llano River is considered an "ecologically significant stream" by the Texas Parks and Wildlife Department on account of the presence of endemic species and its value for providing drinking water to downstream major cities (Broad et al. 2016). Precipitation and underground springs result in year-round flow of the South Llano River and Llano River and only intermittent drying of the North Llano River in summer. Upland land cover types are mostly Oak and Juniper Shrublands composed of a sparse canopy of Ashe juniper *Juniperus ashei* and plateau live oak with other small shrubs common in the understory and Upland Grasslands composed of native and nonnative grasses with a sparse distribution of trees and shrubs. Major riparian land cover types include Floodplain Grasslands and Wetlands, which is composed of common riparian grasses with limited presence of trees and shrubs; Floodplain Hardwood and Mixed Forests with common canopy species including cedar elm *Ulmus crassifolia*, sugar hackberry *Celtis laevigata*, plateau live oak, and pecan *Carya illinoinensis*; and Edwards Plateau Floodplain Shrublands & Barren consisting of mainly disturbed shrublands with associated grasses in the understory (TPWD 2017).

Edwards Plateau ecoregion

The EPE consists of mostly semiarid upland land cover types composed mostly of Ashe juniper and plateau live oak. Numerous rivers, such as the Llano, Guadalupe, and Nueces rivers, are interspersed in the ecoregion, and the forested riparian corridors surrounding the rivers are, anecdotally, the primary axis deer habitat in the ecoregion (Gould et al. 2011). Major land uses include wildlife production for hunting and small parcels of agricultural production situated in riparian zones raising sheep, goats, or cattle or growing hay. A substantial portion of the land area used for wildlife production is enclosed in high-fence game ranches. Although the exact proportion of the EPE that is in high-fence game ranches is unknown, the Texas Hill Country (i.e., the eastern EPE) and South Texas are thought to have similar proportions of high-fenced areas, with at least 18.8% of South Texas under high fence (Patoski 2002).

Methods

Spotlight surveys

We estimated density and abundance of axis deer and white-tailed deer using nocturnal line-transect distance sampling spotlight surveys on 10 randomly selected survey routes in Kimble County, Texas, on public and private roads, totaling 76 km (Figure 1). We randomly selected survey routes by generating a random point (within property boundaries on private properties with approved access or within county boundaries for public road routes) and selecting the nearest available road and randomly selecting the direction to travel the survey route. Although there are inherent biases with using roads in distance sampling surveys to estimate Cervid densities (Collier et al. 2013), the technique is widely used and accepted by many state wildlife management agencies including TPWD (Cain 2020; Kaminski et al. 2020). Route length varied based on private road accessibility and proximity to areas of high human activity (i.e., highways, towns, and homes). We conducted seven spotlight surveys in June, July, and November 2018 and March, June, July, and December 2019. Each survey consisted of conducting distance sampling via spotlighting on all 10 routes except for November 2018 when we did not conduct 5 survey routes (totaling 16 km) because of their inaccessibility caused by a 250-y flooding event in the region. We selected these survey months to coincide with 1) the growing season and when most axis deer bucks were in rut (June and July; Ables 1977), 2) the nongrowing season and immediately following the primary axis deer fawning period in Texas (March; Ables 1977; Howery et al. 1989), and 3) during the white-tailed deer hunting season (November–December). We conducted surveys on nights prior to, and during, a new moon starting at 2130 hours and continuing until 0400 hours the following morning. We randomly selected the order in which individual survey routes were performed each month. We conducted surveys using two observers from a truck driving at 16 km/h.

We recorded 1) species (axis deer, white-tailed deer, or both species), 2) group size (where applicable), and 3) perpendicular distance from the observer to deer for each encounter during the surveys. We used morphological features (e.g., spots on hide of animal and antler morphology), running style, and vocalizations to identify axis deer or white-tailed deer. Observations where species could not be determined (<3% of observations) were omitted from subsequent analyses. We then recorded the number of individuals and herd composition (number of bucks, does, and fawns) for each group observed. We defined a group (axis deer or white-tailed deer) as individuals that were located ~50 m apart, fled to the same location when spooked, or were assumed to be within vocalization range (e.g., became alarmed when an alarm call was made by another individual in the identified group in the nearby area). We identified the location on the survey route in which an observed group was located perpendicular to the survey route by using a compass to identify the location in which the bearing to the front of truck and the bearing to the observed group were 90° apart. Once the truck was present at that location, we recorded the distance and bearing to the observation. Additionally, for axis deer only, we recorded a global positioning system (GPS) location on the survey route.

Geospatial methods

We used ArcMap 10.7.1 (Esri, Redlands, CA) with the GPS data for axis deer to 1) estimate their location(s) during surveys and 2) identify the associated land cover type at those axis deer locations. We created a 225-m flat-ended buffer (hereafter, survey area) around each survey route. We selected 225 m as the buffer radius because that was the farthest recorded distance of an observed group of axis deer during surveys (Faas and Weckerly 2010). We imported the GPS point for each observation of axis deer recorded during the surveys into ArcMap and then drew a perpendicular line from the survey route at this location using the azimuth and distance recorded during the survey to obtain the estimated location of the observed axis deer group and its associated land cover type (Anderson et al. 2013). To obtain random locations for subsequent selection analyses, we generated an equal number of randomly selected points ($n = 321$) within the survey area using ArcMap to the number of observations of axis deer groups identified during spotlight surveys.

We used the Texas Ecological Analytical Mapper (TEAM) geographic information system layers created by TPWD in conjunction with data from the Landscape Ecology Program of TPWD to assess land cover type affiliated with each detection (TPWD 2017). We extracted the land cover type at each estimated observed and random location from the TEAM layer using the "Extract Values to Points" tool in ArcMap to include as a covariate in the density assessment for axis deer. Of the 20 identified land cover types present in Kimble County, 17 (85%) were represented in the survey area, and axis deer were recorded in 15 (75%) of the land cover types present within the county.

Table 1. Number and percent of total of axis deer *Axis axis* groups observed, individuals observed, area in the survey area (km^2), and area in Kimble County, Texas (km^2), among nine land cover types during spotlighting distance sampling surveys to assess axis deer density in Kimble County, Texas, 2018–2019.

Land cover type	Group observations, *n* (% of total)	Individuals observed, *n* (% of total)	Area in survey area, km^2 (% of total)	Area in Kimble County, km^2 (% of total)
Edwards Plateau Deciduous Shrublands	7 (2.2)	28 (1.6)	0.80 (2.4)	119.4 (3.7)
Upland Grasslands	67 (20.9)	388 (21.6)	5.18 (15.2)	360.8 (11.1)
Floodplain Grasslands and Wetlands	27 (8.4)	200 (11.2)	1.71 (5.0)	38.6 (1.2)
Floodplain Hardwood and Mixed Forests	45 (14.0)	233 (13.0)	1.54 (4.5)	28.6 (0.9)
Edwards Plateau Floodplain Shrublands & Barren	14 (4.4)	125 (7.0)	1.08 (3.2)	25.1 (0.8)
Oak and Juniper Shrublands	78 (24.3)	426 (23.8)	12.34 (36.3)	1,686.9 (52.1)
Live Oak Forests and Woodlands	35 (10.9)	138 (7.7)	3.17 (9.4)	376.6 (11.6)
Mesquite Shrublands	14 (4.4)	80 (4.5)	2.53 (7.5)	144.2 (4.5)
Urban Low Density	20 (6.2)	121 (6.8)	1.26 (3.7)	32.1 (1.0)
Other land cover types not included in analyses	14 (4.4)	54 (3.0)	4.34 (12.8)	425.1 (13.1)
Total	321 (100)	1,793 (100)	34.0 (100)	3,237.4 (100)

Density and detection probability estimations

We calculated axis deer and white-tailed deer density and detection probability estimates using Program DISTANCE 7.3 release 2 (Thomas et al. 2010). We used a two-tiered approach and Akaike's Information Criterion for small sample sizes (AIC_c), ΔAIC_c values, and Akaike weights (w_i) to select the best density predicting model for both species independently (Anderson et al. 2000). The first tier was to assess the appropriate combination of key function and series expansion by altering these parameters in DISTANCE for different classes of models that separately included no covariates (i.e., conventional distance sampling), a group size covariate only, a land cover type covariate only (axis deer only), and both covariates (axis deer only). Before conducting the distance analyses for axis deer, we removed 6 land cover types (14 total observations of axis deer) because each type had ≤ 6 recorded observations (Table 1). Therefore, only 9 of the 15 land cover types with recorded observations of axis deer (87.2% of the total area of the survey area) and 307 of the 321 total observations (95.6%) of axis deer were included in the analyses (Table 1). The group size covariate was binned into four levels corresponding to 1–4 individuals, 5–10 individuals, 11–20 individuals, and 21+ individuals. The second tier consisted of comparing the top models from each of the classes of models from the first tier to identify which class of model (i.e., conventional or a specific covariate) best predicted density for each species. We used the poststratify option in DISTANCE to define strata in the model as the month the survey was conducted and specified that strata were replicates where overall estimated density was the mean of replicates. We calculated estimated density and 95% confidence intervals using 2,500 repetitions of bootstrap resampling of samples within strata.

We also estimated density and detection probabilities for axis deer in individual land cover types. We included group size as a covariate in the land cover type-specific models only if the second tier of the model selection process above included group size within the overall top competing model. We calculated densities and 95% confidence intervals for each individual land cover type using 2,500 repetitions of bootstrap resampling of samples within strata. We calculated a weighted global density by averaging the individual land cover type densities weighted by area within the survey area. The proportion of the survey area that was not included in the individually estimated land cover types was accounted for by including a density of zero axis deer/km^2 for the remaining portion of the survey area. This resulted in two separate estimates of density of axis deer, one from the top overall model in the model selection process described above and one calculated with densities in different individual land cover types weighted by the availability of the land cover types.

Data S1, *Supplemental Material,* includes the data used to estimate axis deer density both globally and in individual habitats. This includes the habitat where the observation was made, survey route IDs and lengths, perpendicular distance, total individuals in the group, both the group size and habitat covariates, and the survey period. We omitted precise GPS coordinates of observed locations of groups of axis deer to provide privacy to private properties where surveys were conducted. Data S2, *Supplemental Material,* includes the data used to estimate white-tailed deer density. This includes the survey route IDs and lengths, perpendicular distance, total individuals in the group, the group size covariate, and the survey period.

Habitat selection index

We used a one-way chi-square test to assess whether land cover types were used by axis deer in proportion to what was expected as represented by the randomly selected points. We then calculated a 95% confidence interval for each land cover type centered on the proportion of observed groups in each land cover type using the following equation:

$$\hat{p} \pm 1.96\sqrt{\hat{p}\hat{q}/n}$$

(Zar 2010) where $\hat{p}$ = the proportion of the total observations that occurred in that land cover type; $\hat{q}$ =

Table 2. Number of observations of axis deer *Axis axis* and white-tailed deer *Odocoileus virginianus* during spotlighting distance sampling surveys in Kimble County, Texas, 2018–2019 during seven survey periods. The number of individuals and group observations removed from distance analyses for axis deer was because they occurred in land cover types with less than or equal to six recorded observations.

	No. of survey routes conducted	Axis deer: Groups observed (*n*)		Axis deer: Individuals observed (*n*)		White-tailed deer	
		No. used in analyses	No. removed from analyses	No. used in analyses	No. removed from analyses	Groups observed (*n*)	Individuals observed (*n*)
June 2018	10	63	1	394	14	205	291
July 2018	10	63	3	379	9	178	307
November 2018	5	29	1	201	1	123	228
March 2019	10	44	4	248	11	92	237
June 2019	10	37	0	164	0	128	222
July 2019	10	37	3	211	17	128	218
December 2019	10	34	2	142	2	92	205

one minus the proportion of the total observations that occurred in that land cover type; and $n =$ the number of observations in that land cover type. We considered land cover types to be used more or less than expected if the chi-square test was significant ($P < 0.05$) and the expected number of points fell outside of the observed 95% confidence interval (see Fritts et al. 2016).

Population extrapolation and growth

We estimated the total population size of axis deer in Kimble County by using the estimated densities from individual land cover types in the survey area extrapolated to the study area of Kimble County. We multiplied the total area of each land cover type (km^2) in the Kimble County TEAM habitat layer in ArcMap by the estimated number of axis deer/km^2 for each land cover type individually. Then, we found the 95% confidence interval of population size for each land cover type by multiplying total area of each land cover type (km^2) in Kimble County by the lower and upper limits of the 95% confidence interval of density in each habitat individual type. We then calculated the total population estimate and 95% confidence interval by summing the estimated population sizes of all eight individual habitats (see Buckland et al. 2001 for similar procedure).

To model the potential for population growth of axis deer in Texas, we estimated the intrinsic rate of increase for axis deer in Texas by solving for r_{max} with the following equation:

$$r_{max} = \log[(n8 \times t8)/(n1 \times t1)]/(t8 - t1)$$

(Zar 2010). We estimated r_{max} with the population estimates obtained by TPWD from 1966 to 1994 (Traweek 1995) where n8 is the estimated number of axis deer from the last TPWD survey in 1994 (t8). We used an initial population size of $N = 10$ (n1) axis deer to simulate the approximate number of individuals released in 1932 (t1). The number of individuals initially introduced in 1932 is unknown, but is believed to be relatively few individuals. Therefore, we used 10 individuals as the assumed initial population size, so the estimate of r_{max} would be as conservative as possible.

Results

Survey results

We conducted 65 distance surveys over seven survey periods, where 321 groups (1,793 individuals) of axis deer and 946 groups (1,708 individuals) of white-tailed deer were observed for all surveys combined (Table 2). The average number of observations of groups and individual axis deer per survey period was 45.9 and 256.1, respectively, whereas the averages for white-tailed deer were 135.1 and 244, respectively. Overall detection probability, obtained from the results of top models of the model selection process described below, of axis deer was 0.38 (95% CI: 0.34–0.41), whereas overall detection probability of white-tailed deer was 0.33 (95% CI: 0.31–0.35).

Density estimates from model selection process

For axis deer, the combination of hazard rate key function and cosine series expansion had the lowest AIC$_c$ value for all four classes of models (Table S1, *Supplemental Material*), whereas the second tier of model selection indicated that the top overall model from the four classes of models included only the land cover type covariate (Table S2, *Supplemental Material*). The estimated axis deer density from the land cover type covariate model was 19.7 (95% CI: 14.1–25.6) axis deer/km^2. Individual survey period density estimates ranged from 9.1 to 36.4 axis deer/km^2. Although density of axis deer was estimated to be greatest in June 2018 and July 2018 relative to any other survey period, confidence intervals overlapped with the other survey periods (Table 3).

Conventional distance analysis with a key function of hazard rate and series expansion of simple polynomial was most appropriate to estimate density of white-tailed deer (Tables S3 and S4, *Supplemental Material*). The estimated white-tailed deer density from the conventional model was 23.0 (95% CI: 18.2–27.5) white-tailed deer/km^2. Individual survey period density estimates varied between 18.5 and 29.5 white-tailed deer/km^2. Similar to axis deer, white-tailed deer density

Table 3. Density of individuals of axis deer *Axis axis* and white-tailed deer *Odocoileus virginianus* estimated from spotlighting distance sampling surveys in Kimble County, Texas, 2018–2019 during seven survey periods. Values in parentheses depict the 95% confidence intervals of density.

	Density of axis deer (individuals/km^2)	Density of white-tailed deer (individuals/km^2)
June 2018	31.4 (12.5–57.8)	28.4 (18.0–39.6)
July 2018	36.4 (12.8–71.0)	29.5 (17.7–42.4)
November 2018	9.1 (0.6–17.3)	18.5 (6.3–27.8)
March 2019	18.0 (10.9–25.9)	21.3 (9.4–33.1)
June 2019	13.8 (1.1–25.6)	19.7 (7.4–33.5)
July 2019	15.6 (6.4–25.1)	20.9 (9.8–30.3)
December 2019	14.6 (4.9–23.5)	21.1 (9.2–32.1)

was estimated to be greatest in June 2018 and July 2018 relative to any other survey period; however, confidence intervals overlapped with the other survey periods (Table 3). By summing the separately estimated densities of both species, the total density of both cervid species in Kimble County was calculated as 42.7 deer/km^2.

Axis deer density estimates from land cover types

We did not calculate an individual density for the Urban Low Density land cover type because its distribution was limited to county and state roads and highways. Therefore, observations included in this classification all had short observational distances (range = 0–39 m) because axis deer were on or near the roadside. One of the primary assumptions of distance sampling is that all animals along the line transect are observed, so these short distances artificially biased density estimates positively in this classification of land cover type and we dropped it from individual analysis to minimize positive bias.

The top model from the second tier of the model selection process did not include the group size covariate; therefore, we did not include the group size covariate in the individual land cover type density models. The three (Floodplain Grasslands and Wetlands; Floodplain Hardwood and Mixed Forests; and Edwards Plateau Floodplain Shrublands & Barren) riparian land cover types all had densities $\geq$1.62 times greater than any of the five upland habitats. However, confidence intervals of individual density overlapped for all eight land cover types (Table 4). Weighted global density was 25.5 (95% CI: 10.1–46.9) axis deer/km^2. The estimated Kimble County population size was 61,078 (95% CI: 30,407–100,369) total axis deer in the eight individual land cover types, which together account for 85.9% (2,780.22 of 3,237.39 km^2) of the spatial extent of Kimble County, Texas.

Habitat selection index

We recorded 321 observations of axis deer groups during spotlight surveys and generated an equal number of random points within the survey area in ArcMap.

Table 4. Density of groups and individuals of axis deer *Axis axis* in eight individual land cover types estimated from spotlighting distance sampling surveys in Kimble County, Texas, 2018–2019. Values in the parentheses depict the 95% confidence intervals of density and detection probability estimates. An asterisk (*) indicates an upland land cover type, whereas a dagger (†) indicates a riparian land cover type.

	Groups/km^2	Individuals/km^2
Edwards Plateau Deciduous Shrublands*	8.1 (4.3–14.7)	30.9 (13.8–59.0)
Edwards Plateau Floodplain Shrublands & Barren†	7.5 (3.3–12.3)	171.0 (17.9–271.2)
Floodplain Grasslands and Wetlands†	5.7 (3.7–8.2)	50.1 (17.6–183.1)
Floodplain Hardwood and Mixed Forests†	12.3 (4.9–21.2)	64.0 (20.2–131.1)
Live Oak Forests and Woodlands*	4.8 (3.3–6.4)	20.5 (11.8–36.9)
Mesquite Shrublands*	3.5 (1.5–6.2)	22.7 (7.6–43.7)
Oak and Juniper Shrublands*	3.4 (2.1–4.5)	16.9 (9.5–24.3)
Upland Grasslands*	4.6 (3.1–6.2)	27.4 (15.1–40.5)
Weighted Global Estimate	—	25.5 (10.1–46.9)

Observed land cover type use was not equal to the expected land cover type use ($\chi^2_{16} = 667.101$, $P < 0.001$). Therefore, we compared the expected proportion of land cover type use to the 95% confidence interval of observed land cover type use for each of the 17 land cover types represented in the survey area to identify land cover types that axis deer used in greater (i.e., selected), lesser (not selected), or with similar (i.e., neither selected or not selected) proportion to that expected (Figure 2). The three land cover types that were selected comprise 13.2% (428.00 km^2 of 3,237.39 km^2) of the study area. The six land cover types that were not selected comprise 68.1% (2,205.99 km^2 of 3,237.39 km^2) of the study area.

Axis deer population growth potential

The estimates obtained by TPWD from 1966 to 1994 (Traweek 1995) demonstrate an increasing trend in axis deer populations in Texas (Figure 3). Using the population estimates and a simulated initial introduction of 10 individuals in 1932 the intrinsic rate of increase (r) of axis deer was estimated to be 0.20. Therefore, it is theoretically possible that the population could increase by up to 20%/y in the absence of regulating or limiting factors slowing population growth.

Discussion

Overall axis deer and white-tailed deer density estimates were similar in the study area, supporting the substantial growth of the axis deer population in Texas, not only from the initial introduction in 1932 but also from the last attempt to estimate axis deer abundance in 1994 (Ables 1977; Traweek 1995). Estimated axis deer density was approximately 85% of the overall estimated density of white-tailed deer, suggesting regional axis deer and white-tailed deer population sizes are likely similar. Axis deer densities among the

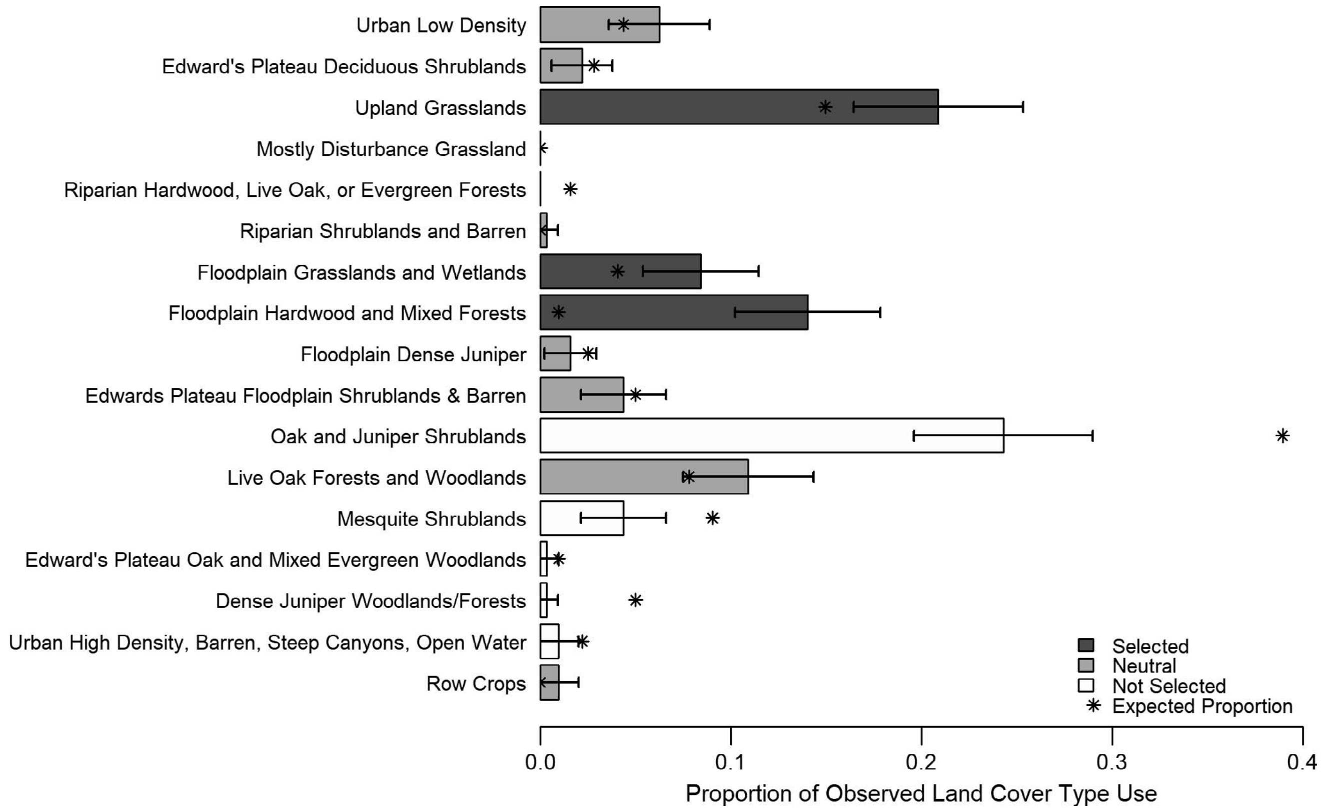

Figure 2. Results of a habitat selection index of axis deer *Axis axis* observed during spotlight surveys in Kimble County, Texas, from 2018 to 2019. Habitats are color coded to represent whether the particular habitat was selected, not selected, or neutral.

different land cover types imply that axis deer may be selecting for sensitive riparian habitats regionally, which remain a conservation issue relative to riparian habitat and water quality management (Boyce et al. 2016; see Broad et al. 2016). Furthermore, the combined estimate of 42.7 deer/km^2 would be extremely high for Cervids without some negative impact on vegetation communities, and it is possible that the high densities reported herein may result in overutilization of shared resources between the two species (Wiggers and Beasom 1986;

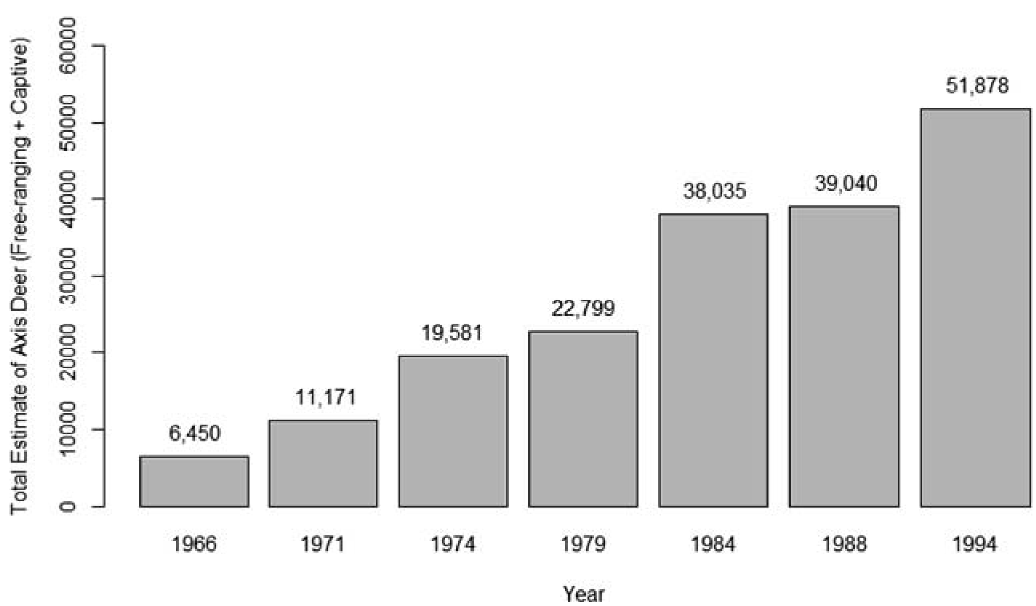

Figure 3. Estimates of total axis deer *Axis axis* population size obtained by Texas Parks and Wildlife Department from 1966 to 1994 (Traweek 1995).

Waller and Alverson 1997; Horsley et al. 2003). This revelation is especially poignant given that the study area of Kimble County, Texas (and the extended area of the Edwards of Plateau Ecoregion) already has some of the highest densities of white-tailed deer in Texas and the addition of a similar density of axis deer could exacerbate habitat impacts by the high summed density of both species (Cain 2020).

Axis deer and white-tailed deer use similar land cover types, including those with dense cover and food resources (Ables 1977; Elliott and Barrett 1985; Henke et al. 1988). Resource competition typically is greatest when densities of animals are maximized and resources are limited (Stewart et al. 2002). Within the context of axis deer and white-tailed deer interactions, Faas and Weckerly (2010) suggested that high densities of axis deer and white-tailed deer would likely result in axis deer outcompeting and displacing white-tailed deer from selected high-value locations like supplemental feeders and optimal land cover types via interference competition. Similar densities of axis deer and white-tailed deer, with the previous supposition that coexistence of these two species at smaller spatial scales is not possible (particularly if the density of axis deer continues to increase; Faas and Weckerly 2010) likely indicates that white-tailed deer may have trouble accessing shared resources when axis deer are present. Faas and Weckerly (2010) also suggested similar densities of the two species may result in a vortex effect, where white-tailed deer abundance may decline, and axis deer may concomitantly become even more abundant, further increasing the impacts of competition upon white-tailed deer. The prospect of a vortex effect is supported by past results in a pen setting where axis deer and white-tailed deer were housed together in a 38.8-ha enclosure at the Kerr Wildlife Management Area in Texas (Baccus et al. 1985). Although both species started with the same number of individuals, white-tailed deer numbers ultimately declined while axis deer numbers increased (Baccus et al. 1985), supporting that as axis deer densities increase, there is a potential to result in decreasing density and abundance of white-tailed deer. Additionally, the similarity of axis deer and white-tailed deer densities is alarming given that axis deer have a higher animal unit equivalency than white-tailed deer, and therefore a similar density of axis deer could have greater habitat impacts than the same density of white-tailed deer (Nelle and Reinke 2011).

Surprisingly, densities of both species were similar among survey periods despite at least two large-scale events that either displaced or were potentially a direct source of mortality for axis deer in the study area (Table 3). First, a 250-y flooding event of the North and South Llano rivers occurred during October 2018. It is possible that the flooding may have resulted in a decline in density of both species by temporarily displacing axis deer and white-tailed deer from riparian land cover types to upland land cover types or via direct mortality. It also may be reasonable to attribute the large decline in the density of both species from July 2018 to November 2018 (Table 3) to flooding that prevented access to several of the survey routes (Table 2) and subsequently a reduced number of observations. However, that may be unlikely because neither species substantially increased in March 2019 and beyond when surveys were resumed. Secondly, there were reports of substantial trapping and removal of axis deer in the study area in October 2018. Approximately 3,000 axis deer were trapped within a 16-km radius of the Texas Tech University Junction Campus in Kimble County between July 2018 and September 2018 (R. Stubblefield, Texas Tech University @ Junction, personal communication). A substantial decrease in axis deer density was expected after these removals, but overlap in confidence intervals of estimated densities temporally did not support those expectations.

Collectively, these factors might indicate that potential mortality from the flooding event may have affected density of both axis deer and white-tailed deer similarly and suggest extreme natural events in the introduced range in Texas that axis deer would be unlikely to experience in India may help to control axis deer populations at local or regional scales. Similarly, an unprecedented period of cold weather in Texas during early February 2021 is suspected to have substantially affected axis deer with very minimal impacts on white-tailed deer. Numerous landowners and stakeholders provided anecdotal estimates that suggested 20–30% mortality rates of axis deer but very few, if any, cases of mortality of white-tailed deer at localized scales (e.g., individual private ranches; B. Slabach, Trinity University, personal communication). However, the occurrence of such natural extreme weather events is not regular enough to be a reliable means by which to control axis deer populations without other aid from human actions.

This study supports the notion that axis deer have largely become ubiquitous throughout the different land cover types in the study area. No individually estimated land cover type had a density $<$16.9 axis deer/km^2 (Table 4), suggesting axis deer are present in significant abundance in many of the land cover types in the study area. Although confidence intervals overlapped (likely as a result of sample size of observations in each land cover type), in general, axis deer were more abundant in riparian shrublands compared with riparian forests and grasslands as indicated by greater estimated densities (Table 4). Furthermore, axis deer also displayed greater densities in riparian land cover types than upland land cover types, where these highly productive riparian habitats were also selected by axis deer in this study. Similar to a study of axis deer in Australia, where density across the entire landscape was relatively low but some localized densities were $>$170 axis deer/km^2 (Watter 2019), densities varied among different land cover types in this study (up to 171.0 axis deer/km^2). Although some localized densities in specific land cover types in this study were high, the limited availability of those land cover types and lower densities in more common land cover types contributed to a lower overall weighted average density (Tables 1 and 4). Compared with white-tailed deer that are a true habitat generalist (Demarais et al. 2000), these findings support previous research that suggests that although axis deer may have a preference for certain land cover types (i.e., riparian habitats and more open cover), they can occur in high numbers in numerous diverse land cover types (Eisenberg and Lockhart 1972; Berwick 1974), and can, and have, become habituated to the ecoregion and are able to persist and thrive in high densities in multiple disparate land cover types.

As expected, given past research on the species (Moe and Wegge 1994; Bhat and Rawat 1995; Sharma and Chalise 2014), axis deer in Texas selected two different riparian land cover types including grasslands and relatively open hardwood forests (Figure 2; TPWD 2017), but not shrublands and more dense forest (Figure 2; TPWD 2017). Although axis deer will use more densely vegetated land cover types, they are primarily considered to prefer more open land cover types for feeding and predator avoidance (Mungall and Sheffield 1994; Faas and Weckerly 2010). Axis deer in this study also selected upland grasslands, which is also a more open land cover type. However, the selection index was developed using locations obtained during nocturnal surveys, so it is possible that the selection of more open land cover types by axis deer was affected by a greater probability of detection of axis deer in the open land cover types compared with more densely vegetated land cover types during the surveys. Conversely, the results of the nocturnal surveys could also have been influenced by nocturnal behavior of axis deer where they are more active and foraging at night (Laura 2015) and may use the additional visibility in open land cover types to avoid predators. Additionally, the selection of upland grasslands by axis deer could be a result of axis deer selecting for the best available habitat outside of the riparian zones given the high abundance of axis deer and the relatively low total area of narrow riparian zones compared with the wide availability of upland grasslands. If or when the axis deer population reaches densities where it has saturated the desirable riparian land cover types then it may be forced to disperse into the most desirable of the overall low desirable upland land cover types (compared with riparian land cover types) that would not otherwise be occupied. Furthermore, with axis deer not selecting for the majority of the landscape, it could put additional pressure on land cover types that are selected or are neutral. Much of the total axis deer population is occupying land cover types that are less abundant, but in greater densities; therefore, axis deer have the potential to have negative impacts (e.g., high levels of herbivory) on those land cover types. This is especially important in selected riparian land cover types because negative impacts of axis deer in these highly sensitive and ecologically important riparian habitats would be highly detrimental to the health of the ecosystem as a whole (Naiman and Decamps 1997).

The clustered density of, and selection by, axis deer of certain land cover types is particularly concerning for sensitive riparian habitats. The high densities of axis deer in riparian land cover types may be detrimental to the health of these habitats via ungulate herbivory, where axis deer remove sensitive vegetation that maintains soil stability and/or serves as food for other native wildlife species (Zuazo and Pleguezuelo 2008; Davis et al. 2016). The riparian corridors in the region are composed of the Nuvalde–Dev–Frio soil series, and these soils are deep, loamy, and gravelly (Broad et al. 2016). These soils can be destabilized by the removal of vegetation that holds the soils stable, particularly as the rivers in the region continue to erode into established cut banks. Furthermore, axis deer also have a propensity for using the same trails day after day, potentially further contributing to detrimental erosion of riparian soils (Schaller 1967; Zuazo and Pleguezuelo 2008). Maintaining the current density of axis deer (or even an increase in density) is likely to cause substantial impacts on the health of riparian habitats that are critical to the socio-economic and cultural identity of the ecoregion, are important water sources for human consumption (drinking water and agriculture), and are important habitat for numerous taxa (Shelton et al. 2014; Broad et al. 2016).

The population estimate of axis deer obtained in this study provides the first estimate of axis deer population size in Texas since 1994 (Traweek 1995) as well as the first ever empirical estimate of axis deer population size in Texas given that previous estimates were based on anecdotal reports. The estimate of 61,078 axis deer in Kimble County exceeded the 1994 estimate of $\sim$5,200 total axis deer in Kimble County by a factor of 12, and exceeded the previously reported state-wide total of $\sim$52,000 ($\sim$23,000 of which were free-ranging) axis deer in Texas reported in the same survey (Traweek 1995), which implies that axis deer in Texas have experienced rapid and substantial growth. Furthermore, although we calculated r_{max} as 0.20 it is possibly much higher given the population growth rate indicated here, which in turn could have substantial impacts on native habitats and wildlife. The slow initial growth rate followed by a much higher growth rate well after axis deer were introduced is not overly surprising given that axis deer have previously been shown to experience a lag period in population growth of introduced populations (Kelly et al. 2021).

Several factors have likely contributed to the population growth of axis deer in the region during the $\sim$30 y. Reproductive traits including the ability of does to become pregnant every 9 mo (Ables 1977; Schmidly and Bradley 2016), year-round breeding potential of does (when not pregnant; Ables 1977; Schmidly and Bradley 2016), possible viability of sperm year-round regardless of antler status in bucks (Willard and Randel 2002), and longevity records in the state that suggest axis deer can live to $\geq$15 y old with pregnancy possible until $\geq$13 y old (see Buchholz 2022) have likely combined to support the rapid growth in axis deer abundance during the past 30+ y. Furthermore, as an introduced species, axis deer likely experience enemy release (see Blossey 2011). Most axis deer fawns ($\sim$75%) in Texas are born between December and March, whereas white-tailed deer fawns in Texas are typically born during May and June (Ables 1977; Howery et al. 1989). The temporal differences in fawning season between these species likely benefits axis deer. For example, the only abundant predators in the EPE region—coyotes *Canis latrans* and bobcats *Lynx rufus*—have coevolved with white-tailed deer, and timing of white-tailed deer fawning during May and June coincides with provisioning for kitten and pups, whereby axis fawns might be spared from high levels of predation because of this temporal mismatch.

Axis deer possess numerous characteristics associated with successful colonization and establishment of introduced vertebrate species (Ehrlich 1989). Collectively, they have demonstrated rapid population growth, generalized food habits, the ability to persist in numerous land cover types, a release from predators, potential preadaptation to the EPE due to similar environmental characteristics (temperature and precipitation) to those of their native range in India, and competitive superiority to native white-tailed deer. Beyond these ecological and biological drivers, their intentional movement and translocation by humans in Texas has provided new colonization opportunities (as well as the initial colonization) more quickly than would be available if only allowed to expand naturally. As a consequence of the successful establishment and spread of axis deer in Texas, they likely are having impacts on native white-tailed deer and habitats (Davis et al. 2016). Ultimately, the potential for introduced axis deer to have these impacts has likely slipped under the radar of wildlife managers because of the popularity of the species on game farms, which may have larger implications for the management of other introduced species that are popular targets for hunting.

Complete eradication of axis deer in Texas is likely no longer possible (Sakai et al. 2001; Allendorf and Lundquist 2003). Therefore, additional population surveys in other areas and increased control efforts and additional methods for removal are warranted to estimate regional density and abundance and control densities of free-ranging axis deer in the EPE to minimize potential ecological impacts. Axis deer are an unmanaged, nonnative species (TPWD 2021b); therefore, management and control of axis deer in Texas is pursuant of individual landowners and may be maximized by increasing cooperation between adjacent private landowners. Therefore, we recommend cooperation among private landowners to help manage primary population processes between and among individual ranches (Gürtler et al. 2017), which with coordinated efforts may impact regional densities of axis deer. Management actions we recommend include, but are not limited to, increasing female axis deer harvest rates (Boulanger et al. 2011), large-scale trapping and removal by professional trappers or biologists, increasing axis deer harvest on private property via publicly incentivized hunts (Gürtler et al. 2017), large-scale removal via helicopter, and increasing market rates for exotic game meat in near-by major cities (Rubino 2014). Additionally, we are continuing efforts to further estimate axis deer density among private ranches to assess habitat conditions associated with different axis deer densities. We are also replicating the land cover type density and selection component of this research on white-tailed deer to further assess the potential negative correlation of axis deer and white-tailed deer densities and the displacement of white-tailed deer by axis deer in particular land cover types.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Data S1. Data collected from spotlight surveys of axis deer *Axis axis* in Kimble County, Texas, from 2018 to 2019 imported into program distance to estimate density of axis deer globally and in individual habitats.

Available: https://doi.org/10.3996/JFWM-22-036.S1 (40 KB XLSX)

Data S2. Data collected from spotlight surveys of white-tailed deer *Odocoileus virginianus* in Kimble County, Texas, from 2018 to 2019 imported into program distance to estimate density.

Available: https://doi.org/10.3996/JFWM-22-036.S2 (38 KB XLSX)

Table S1. First-tier results of AIC_c model selection of four classes of models to assess the top model within each class in program distance to estimate density of axis deer *Axis axis* in Kimble County, Texas, from 2018 to 2019.

Available: https://doi.org/10.3996/JFWM-22-036.S3 (18 KB XLSX)

Table S2. Second-tier results of AIC_c model selection comparing the top models from four classes of models to assess the overall top model in program distance to estimate density of axis deer *Axis axis* in Kimble County, Texas, from 2018 to 2019.

Available: https://doi.org/10.3996/JFWM-22-036.S3 (18 KB XLSX)

Table S3. First-tier results of AIC_c model selection of two classes of models to assess the top model within each class in program distance to estimate density of white-tailed deer *Odocoileus virginianus* in Kimble County, Texas, from 2018 to 2019.

Available: https://doi.org/10.3996/JFWM-22-036.S3 (18 KB XLSX)

Table S4. Second-tier results of AIC_c model selection comparing the top models from two classes of models to assess the overall top model in program distance to estimate density of white-tailed deer *Odocoileus virginianus* in Kimble County, Texas, from 2018 to 2019.

Available: https://doi.org/10.3996/JFWM-22-036.S3 (18 KB XLSX)

Reference S1. Cain A. 2020. Big game research and surveys white-tailed deer harvest recommendations. Austin: Texas Parks and Wildlife Department. Performance report, federal aid project No. W-127-R-23.

Available: https://doi.org/10.3996/JFWM-22-036.S4 (6.404 MB PDF)

Reference S2. Eisenberg JF, Lockhart M. 1972. An ecological reconnaissance of Wilpattu Nation Park, Ceylon. Washington, D.C.: Smithsonian Contributions to Zoology. Publication 101.

Available: https://doi.org/10.3996/JFWM-22-036.S5 (5.227 MB PDF)

Reference S3. Nelle S, Reinke S. 2011. Animal Unit Equivalent Chart – Texas Domestic Livestock, Native Wildlife, and Exotic Wildlife. College Station: Texas A&M AgriLife Extension Service.

Available: https://doi.org/10.3996/JFWM-22-036.S6 (4.835 MB PDF)

Reference S4. Traweek MS. 1995. Statewide census of exotic big game animals. Austin: Texas Parks and Wildlife Department.

Available: https://doi.org/10.3996/JFWM-22-036.S7 (6.192 MB PDF)

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