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Cropland restricts occurrence and alters spatial ecology near the mule deer geographical range limit

Levi J. Heffelfinger[1,5*], David G. Hewitt[1], Joshua P. Vasquez[1,6], Timothy E. Fulbright[1], Randy W. DeYoung[1], Louis A. Harveson[2], Warren C. Conway[3] and Shawn S. Gray[4]

Abstract

Background Habitat fragmentation can influence the spatial ecology of wildlife populations, with downstream effects on population dynamics and sustainability. Row-crop farming is a common anthropogenic landscape alteration, yet the effects on animal movement and space use is understudied in some species. Cropland can benefit wildlife nutritionally but may result in habitat loss because of changes in landscape composition and human disturbance.

Methods We quantified the influence of cropland presence and coverage on mule deer spatial ecology in the southern Great Plains. We GPS-collared 146 adult mule deer in four regions of the Texas Panhandle and monitored movement relative to spatio-temporal fluctuations in cropland and particular crop species availability for 2 years. We modeled the effects of cropland on space use and resource selection at multiple spatio-temporal scales to characterize population and individual habitat components of mule deer.

Results We observed a functional response in cropland use, where at low coverage, use was proportional to availability but decreased with > 20% cropland coverage at the home range and within-home range scales. Few mule deer exhibited long-distance movements towards cropland. Individuals within 1.6 km of cropland exhibited greater cropland use, whereas deer > 4.2 km from cropland rarely used these areas. At the population level, mule deer selected cropland during the winter and late summer, probably for nutritional benefit when rangeland nutrients are low. At a finer scale, step-selection functions identified individual heterogeneity in crop species selection. Winter wheat, alfalfa, and fallow fields had greater use relative to other crop types. Generally, 15–60% of mule deer with access to cropland selected alfalfa year-round, and up to 63% of deer selected winter wheat post-reproduction.

Conclusions Our results suggest that at a low spatial coverage, cropland alters the spatial ecology of mule deer at several spatio-temporal scales and may provide nutritional benefits, but at a cost of lost habitat when cropland exceeds 20% of the landscape. Declining groundwater resources and an exponentially growing human population will alter future farming practices. Understanding how species occupying these environments, such as mule deer, are

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*Correspondence:
Levi J. Heffelfinger
levi.heffelfinger@tamuk.edu

Full list of author information is available at the end of the article

influenced by human-induced landscape changes can enhance mitigation of human-wildlife interactions and aid conservation actions as policy and social pressures shape future agricultural practices.

Keywords Functional response, Resource selection, Step selection, Cropland, *Odocoileus hemionus*, Great plains, Ogallala aquifer, Row-crop farming

Background

Anthropogenic land-use practices capture nearly 50% of global ecosystem production for human uses [1, 2], and habitat fragmentation through changes in natural and cropland landscape composition is an inevitable consequence, posing a severe threat to biodiversity [3, 4]. Landscape-level changes threaten the future of wildlife species in many areas where humans alter habitat [5, 6]. Human-induced landscape changes, including roads [7], mining [8], energy development [9], and logging [10], alter animal space use and movement ecology. Therefore, land-use practices often dictate how animals use the landscape, as wildlife respond to disturbance by altering their distribution and behavior to meet resource requirements [11–13].

The landscape-level human footprint is not restricted to highly urbanized areas, and one of the most extensive anthropogenic changes is the conversion of native rangelands to cropland [2, 14, 15]. Landscapes altered for agriculture now occupy nearly 40% of the planet's land surface, rivaling the extent of forest cover [2, 16]. Specifically, row-crop farming both reduces connectivity of native vegetative communities and may alter nutritional carrying capacity for many species. Cropland coverage and composition differs spatiotemporally and is controlled by land ownership tenure, soil types, irrigation, climate patterns, livestock, topography, and various decisions made by landowners [6]. Landscape heterogeneity produced via row-crop farming has the potential to enact an improvement in landscape productivity and thus foster a greater level of biodiversity [17]. Landscape heterogeneity from cropland can range from highly complex patterns of multiple crop species to extremely intensive cropland systems containing few crop types in large uniform fields [6, 18]. The disparate land-use practices surrounding cropland and how these alter landscape structure has implications for wildlife spatial ecology.

The influence of cropland on animal populations varies, especially effects on animal movements. The reduction of landscape connectivity by farming induces enhanced fragmentation and thus a habitat loss, which often has negative consequences for species such as forest or grassland obligates [19, 20]. Cropland can slow animal movement as the result of landscape heterogeneity [21] or invoke riskier movement in patchy environments, both of which could negatively influence vital rates, such as survival [22]. Conversely, open patchy environments resulting from cropland conversion can facilitate increased movement or dispersal in some species [23, 24], or invoke a functional response which results in density-dependent responses in cropland use where croplands are avoided when their density is greater on the landscape [25]. The conversion of native biotic communities to row-crop farming can have a positive influence on wildlife habitat use, where cropland serves as a nutrition enhancement on the landscape for herbivores [26, 27] and attracts prey for carnivores [28].

The southern Great Plains of North America was one of the most extensive grassland ecosystems in the world but has experienced extensive shifts in landscape composition. Further, cropland in this semi-arid ecosystem is largely facilitated by irrigation from the Ogallala Aquifer, which is rapidly depleting [29–32]. Cessation of irrigation from the Ogallala Aquifer will shift land-use practices by changing the distribution, coverage, and types of croplands [33–35]. The north-western region of Texas, commonly referred to as the Texas Panhandle is experiencing exceptional aquifer depletion rates with some estimates indicating a loss of available groundwater before the year 2100 [30, 36, 37]. This region has high cropland densities intermixed with remnant short grass prairies, shrubland, and river breaks, where many Great Plains animal species still occur. Mule deer (*Odocoileus hemionus*) is one such species, although its range also includes most of western United States [38, 39]. The Great Plains represent the eastern edge of the mule deer geographical range, and few regions exist where both mule deer and dense cropland coincide [27, 39].

Although shifts in habitat heterogeneity from row-crop farming can negatively affect some wildlife species [40], species such as mule deer in the Texas Panhandle seem to benefit from cropland [27]. Mule deer are abundant throughout the region and their populations have increased over the past three decades. Nevertheless, the Texas Panhandle remains the southeastern fringe of the mule deer distribution; meaning regional attributes are somehow limiting species expansion. Some mule deer in the Panhandle obtain 50% of their digestible energy, crude protein, and phosphorus from row-crops [41]. Additionally, anecdotal observations of mule deer congregating on row-crop fields are common and reports suggest mule deer may exhibit movements towards cropland seasonally, though the frequency and extent of such movements have never been investigated. If true, spatially heterogeneous densities of mule deer subsidized by cropland could pose false expectations of abundance in the future or bias current population estimates. Though mule deer in the Panhandle are non-migratory, individuals may make large, exploratory movements outside of their typical home range to acquire resources during certain times of the year. Though the influence of cropland on white-tailed deer (*Odocoileus virginianus*) has been evaluated [24, 42–45], there are only a few instances where row-crop dominated landscapes coincide with the mule deer geographic range, and few studies have directly tested how cropland shapes mule deer spatial ecology [26, 46].

Our objective was to evaluate how a heterogeneous landscape of row-crop farming and rangeland affects mule deer spatial ecology in the southern Great Plains. We hypothesized a spatial limit in cropland coverage and distance exists and predicted that greater cropland coverage limits mule deer cropland use, however, greater distance from cropland limits access to crops. Conceptually, a functional response to cropland coverage may elucidate a landscape complementation of resources, where a need for different resources is not necessarily available in the same area [47]. We further hypothesized mule deer should alter their cropland use relative to cropland availability during times when rangeland nutritive values are low. We predicted availability of crop species may attract or deter mule deer use seasonally. To address our hypotheses, we assessed how relative coverage and distance to cropland influences cropland use by mule deer by exploring functional responses in cropland use relative to changing availability. We then modeled how selection of cover types changed monthly via population-based resource selection functions (RSFs) at the landscape scale and within home range scale using step selection functions (SSFs). Finally, we focused on the variability of mule deer behavior relative to spatio-temporal variation in crop type using individual-based step selection modeling. Our multi-scale approach at both the population and individual level provides a comprehensive understanding of how a relatively novel landscape configuration for mule deer influences the species near the geographical extent.

Methods

Study site

Our study occurred in the northwestern region of Texas commonly referred to as the Texas Panhandle (Fig. 1). The Texas Panhandle is dominated by cropland with areas of sandy shortgrass prairie, deciduous shrubland, caprock escarpments, and river break drainage systems interspersed throughout. Common grass and forb species found throughout the Texas Panhandle are present in our study sites including sideoats gramma (*Bouteloua curtipendula*), blue gramma (*Bouteloua gracilis*), buffalo grass (*Bouteloua dactyloides*), big bluestem (*Andropogon gerardii*), sand verbena (*Abronia villosa*), bush sunflower (*Encelia californica*), prairie clovers (*Dalea spp.*), and scarlet globemallow (*Sphaeralcea coccinea*) [48]. Though trees are not common throughout the Texas Panhandle, primary woody plant species in our sites were shinnery oak (*Quercus havardii*), sand sage (*Artemesia filifolia*), Mohr oak (*Quercus mohriana*), sand plum (*Prunus texana*), honey mesquite (*Prosopis glandulosa*), netleaf hackberry (*Celtis reticulata*), western soapberry (*Sapindus saponaria*), western hackberry (*Celtis occidentalis*), one-seed juniper (*Juniperus monosperma)*, and four-winged saltbush (*Atriplex canescens)* [48]. In descending prevalence order, primary row-crop species in the region consist of cotton (*Gossypium herbaceum*), corn (*Zea mays*), winter wheat (*Triticum aestivum*), alfalfa (*Medicago sativa*), sorghum (*Sorghum bicolor*), peanuts (*Arachis hypogaea*), potatoes (*Solanum tuberosum*), and canola (*Brassica napus*). In this region, winter wheat is grown in the cooler months in an opposite rotation to traditional summer crops; many times, using the same fields after summer crops are harvested to mitigate erosion. Therefore, winter wheat was the only crop available during the winter months (October-April) whereas the rest were available during the summer months (May-September) apart from alfalfa which was available year-round. The predator community relevant to mule deer in this region only consists of coyotes (*Canis latrans*). Historic average temperature values range from a low of -14° C during winter and a high of 33° C during the summer [49]. Annual precipitation is generally 54 cm in the region, of which up to 25 cm can be snowfall [49]. Because of the moderate to low amount of precipitation, nearly all row-crops are irrigated.

We selected 4 sites in the Texas Panhandle that were representative of the southern Great Plains and offered a mosaic of differing cropland densities relative to native rangeland. Nearly all our study areas were privately owned and legal mule deer harvest in the region was conservative in that state regulations allow one mature male harvested annually per license holder. Our first study site was in the southeast portion of the Texas Panhandle in the Western Rolling Plains ecoregion off the eastern edge of the Llano Estacado escarpment, a plateau that facilitates much of the cropland in the region. This site was characterized by interspersed cropland among patches of native rangeland with the northeastern portion of the site exhibiting primarily rolling plains and shrubland. Primary crop species were cotton and winter wheat. The relative cropland coverage was 14.5% land cover, and the terrain was characterized by minor gradients of elevation (mean ± SD; 667.6 m ± 36.0), slope (2.6^0±2.6), relative terrain ruggedness (1.2 ± 1.2), and distance to roads (3416.9 m ± 2417.2). Using the large suite of random locations used in resource selection analyses (see below),

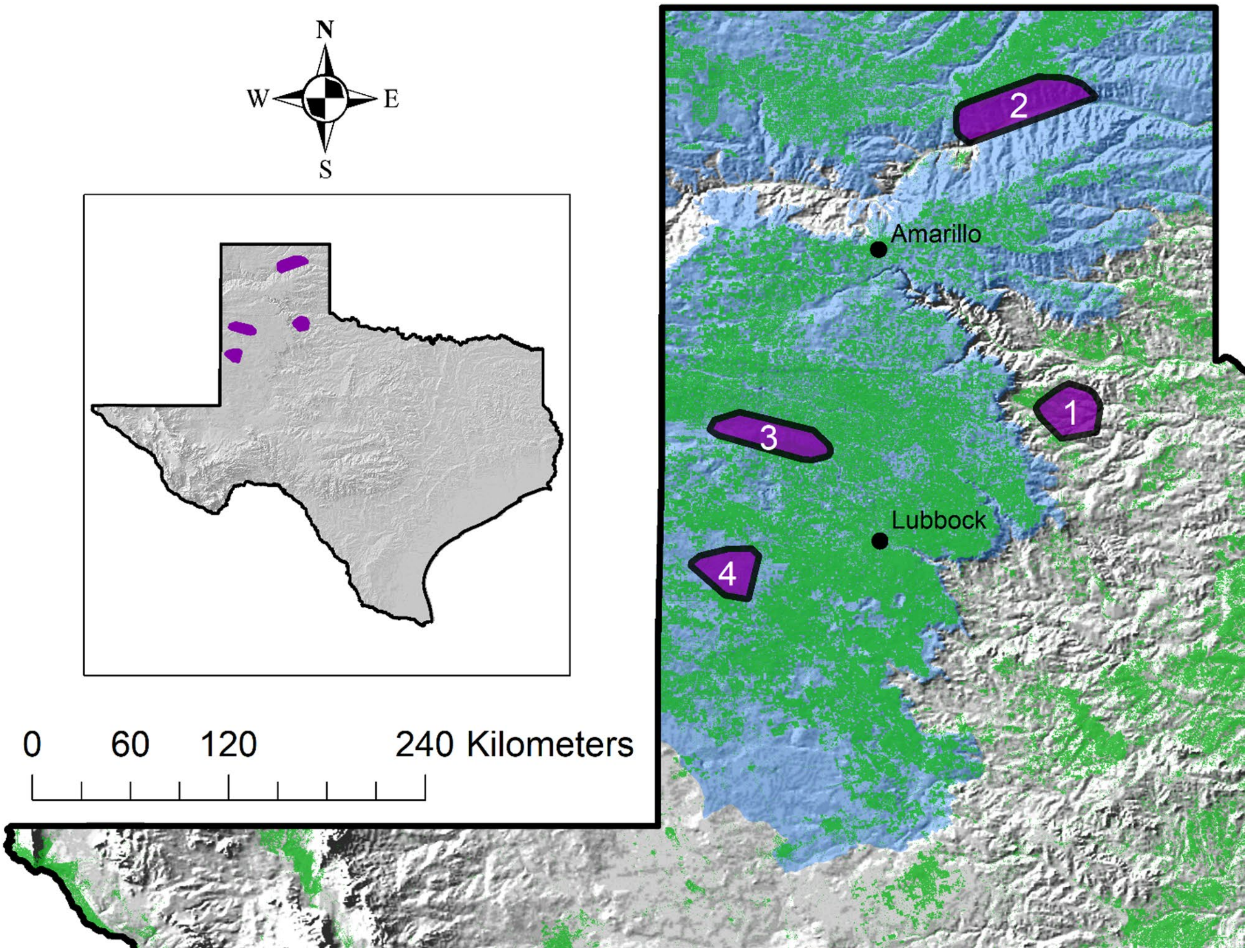

Fig. 1 The Texas Panhandle with four study sites (purple) used to assess the influence of cropland on mule deer spatial ecology using 146 mule deer from 2015–2019. Much of the Panhandle is on a caprock escarpment with very little variation in topography (grayscale) and is dominated by cropland (green) which sits atop the rapidly depleting Ogallala Aquifer (blue)

mean distance throughout this study site to cropland was 2,062 m (Additional File 1). The second study site was in the northeast portion of the Texas Panhandle along the Canadian River Breaks region characterized in the southern portion by riparian corridors along the Canadian River. Moving up in elevation to the north, the site had rolling hills of short grass prairie which eventually lead to steep canyon escarpments. Sitting above the Canadian River system are areas of dense cultivated land with an overall cropland coverage of 11.3% land cover and a mean distance to cropland of 5,166 m (Additional File 2). Terrain was characterized by minor gradients of elevation (880.9 m ± 62.2), slope (3.6^0±4.3), relative terrain ruggedness (1.6 ± 1.9), and distance to roads (6338.8 m ± 4423.0). Crop species in the region consist of cotton, corn, winter wheat, and sorghum. Our third and fourth study sites were in the southwest Texas Panhandle. The third site was characterized by the greatest amount of cropland in this study with interspersed sandy areas where remnant native vegetation communities persist. This area had few trees and was dominated by short-grass prairie species and shrubs. Crop species in the region consist of cotton, corn, winter wheat, alfalfa, and sorghum. Cropland coverage in this study area was 23.9% land cover with a mean distance to cropland of 603 m (Additional File 3). Terrain was characterized by minor gradients of elevation (1121.8 m ± 22.8), slope (0.6^0±0.7), relative terrain ruggedness (0.3 ± 0.3), and distance to roads (1829.5 m ± 1243.0). Lastly, our fourth study site was dominated by rolling sand dunes, many of which were vegetated. Primary crop species were cotton, winter wheat, peanuts, and corn. The relative cropland coverage within this site was 10.4% of the land cover with a mean distance to cropland of 2,427 m (Additional File 4). Terrain was characterized by minor gradients of elevation (1113.9 m ± 19.1), slope (0.5^0±0.6), relative terrain ruggedness (0.2 ± 0.3), and distance to roads (2065.6 m ± 1681.7).

Movement data

From 2015 to 2019, we captured adult male and female mule deer throughout the four study sites using the helicopter net-gun technique [50]. Captured deer were flown to a central processing station for morphometric measurements. We fitted each deer with a GPS radio-collar (Lotek Wireless, GPS3300 or GPS6000, Ontario, Canada) programmed to collect one store on-board GPS location every two hours. Each collar emitted a Very High Frequency (VHF) signal and included a mortality switch. We captured and collared individuals at each study site and collars were active for two consecutive years. After one year of monitoring in each site, we performed a capture to download GPS location data and add individuals to replace mortalities or failed collars. After two years of monitoring, we performed the final capture to remove collars and download the remaining location data. We screened locations to exclude two weeks post-capture, following mortality events, with poor precision confidence (HDOP > 10), and distances from the last location that would have required unrealistic speeds (i.e., > 5 km per hour) [51, 52].

Landscape variables

Though study sites were carefully selected to represent a mosaic of varying cropland densities and crop types, other landscape factors may influence mule deer space use and resource selection. To address this, we gathered landscape variables often predictive of mule deer movement and resource selection including elevation, slope, terrain ruggedness, and distance to roads. We obtained a 30 × 30 m elevation raster from Amazon Web Services Open Data Terrain Tiles dataset (https://registry.opendata.aws/terrain-tiles/) and calculated the percent slope and relative Terrain Ruggedness Index from the "raster" package in R v4.1.1. Lastly, we calculated a distance to roads raster at a 30 × 30 m resolution using road data obtained from Texas Department of Transportation (https://gis-txdot.opendata.arcgis.com).

To characterize when crops were present or absent in our study sites, we physically monitored a sample of 241 unique row-crop fields across our four study sites for the duration of the project. During our monthly visits, we documented crop species present and phenological growth stage as a means of identifying when crop emergence or crop harvest occurred [53]. We spatially referenced and assigned monthly presence of crop species to all 241 monitored fields in ArcGIS (ArcGIS 10.8.1, Environmental Systems Research Institute [ESRI], Redlands, CA, USA). We also georeferenced crop fields that were not directly monitored but were within the study areas. We manually assigned crop species values for each non-monitored field with Cropscape [54] and accounted for variable crop rotation by identifying time of planting and harvest with a combination of data from nearby monitored fields and visual inspection of Planet Imagery monthly satellite images [55]. We then overlaid each monthly crop species prevalence layer onto native land cover data that are updated annually from the Texas Ecological Mapping Systems program [56]. We reclassified our monthly land cover layers into categories including shrubland, grassland, wooded (which includes riparian areas), each individual crop species, and fallow fields (which includes fields enrolled in the Conservation Reserve Program; CRP). We also created a general cropland category including all fields with active cultivated crops or those recently plowed or harvested. For specificity, fallow fields are those that have not been actively used for row-crops in ≥ 2 growing seasons and thus contain native species re-growth similar to that of CRP fields. Classified land cover layers were then transformed into distance raster layers, where the Euclidean distance was calculated for each 30 × 30 m raster pixel per land cover class.

Functional responses to cropland

We evaluated whether mule deer exhibited a functional response in resource use relative to the cropland coverage at multiple spatial scales [47]. There is a large variation in proposed methods to evaluate functional responses in habitat selection, but the universal goal of these approaches is to understand how availability of a resource influences use or selection of that resource [47, 57–59]. Our objectives were to understand the link between cropland availability on the landscape relative to use by collared mule deer. Mule deer are herbivores, and thus proportional use of cropland is roughly equivalent to the time spent foraging in cropland [60]. We wanted to focus on use of cropland resources from a large herbivore's perspective relative to foraging and followed Holbrook et al. [61] by modeling functional responses on the additive scale (% use relative to % available). Within the additive approach, the measure of use is compared to the relative availability across the observed range of values for the given resource [61]. Deviations from a 1:1 relationship of proportional use to availability indicate a functional response (i.e. use changes based upon availability) [61].

We calculated functional responses in cropland use relative to availability at the home range and within home range scales [47, 61]. First, to develop availability at the home range scale, we calculated autocorrelated kernel density estimators (AKDE) using all locations of each individual. AKDEs resolve assumptions surrounding traditional kernel density estimators, where location data are assumed to be identically and independently distributed in time and space [62, 63]. We aimed to maintain our collaring efforts per site by replacing mortalities with new collared individuals. Therefore, the number of locations per individual varied, and traditional home range estimators would tend to be biased [62]. The AKDEs use underlying movement models to inform the kernel density estimator, thereby resulting in a home range prediction that encompasses current and future movement [62, 63]. For each individual, we developed five continuous-time movement models, including Brownian motion, Ornstein-Uhlenbeck process, Ornstein-Uhlenbeck forage process, integrated Ornstein-Uhlenbeck, and an uncorrelated independent data process (analogous to a traditional kernel density estimator) [64]. We then compared movement models for each individual via Akaike's Information Criterion (AIC) and selected the model with the lowest AIC value. For 139 out of 146 total study animals, the Ornstein-Uhlenbeck forage process model best fit our data and thus was used to calculate the AKDE. The uncorrelated independent data process movement model best fit the remaining seven individuals and thus a traditional kernel density estimator (KDE) was fit to calculate their home ranges. As expected in deer movement, the Ornstein-Uhlenbeck forage process model simply implies that our monitored deer exhibited a random walk behavior with correlated velocities and a tendency to restrict space use or return to a centralized area [63, 64]. We used the 95% contour isopleth for each individual's home range as a definition of availability at the home range spatial scale for functional response modeling. Second, we quantified availability within the home range by generating random steps that would also be used for step selection modeling (detailed below) to assess how functional responses may occur at a more finite spatial scale (behavioral decisions within the home range). Availability was characterized by connecting successive GPS locations to obtain a distribution of turning angles (ranging from -pi to pi) and step lengths (straight line distance between successive GPS locations) for each individual. We then drew upon each individual's turning angle and step length distributions to generate 15 available steps per each used step to create an availability dataset within the home range.

After defining availability at the total home range and within home range scales, we calculated proportional use by each individual by dividing the number of locations in cropland by the total number of individual locations collected (analogous for proportional time spent in cropland). Using each individual home range, we calculated the spatial proportion of cropland as our measure of availability at the home range scale. Within the home range, we compared the proportion of used steps in cropland relative to other land cover classes to the proportion of cropland attributed to 15 available steps. We followed Holbrook et al. [61] and developed linear models at the additive scale to assess how use may change across observed availability values. We tested a null hypothesis where the additive difference between use and availability was constant, specifically, a slope coefficient estimate may be statistically greater than or less than one, indicating increasing or decreasing habitat use relative to availability, respectively. Furthermore, we applied second- and third-degree polynomials to our models to assess curvilinear functional response [59, 65]. We compared competing models of simple linear, second order, and third order polynomials using R^2 values to assess best fit [61].

We also employed a modified approach in evaluating functional responses by assessing cropland use based on the distance from an individual's home range centroid to the nearest crop field. We aimed at defining the distance from the home range to the nearest cropland at which a mule deer does not move to use the resource. To predict differences in use relative to home range centroid distances, we employed piecewise regressions; a common tool in identifying ecological thresholds [66]. Piecewise linear models aid in identifying breakpoints in the relationship between the predictor and response variables (i.e., changes in slope values) [67]. We specified three break points for the piecewise models to identify high-intensity use at close distances, the transition to moderate or low use, and where cropland use was null given the greater distance to cropland. Modeling was performed with the "segmented" package in R v4.1.1 [68]. Lastly, we applied piecewise regressions to the aforementioned functional response models at both the home range and within home ranges scales. We specified one break point to statistically determine the threshold to where use departed from a 1:1 relationship with availability.

Population-based resource and step selection

We evaluated landscape attributes that define resource selection by mule deer at the landscape scale (i.e., 2nd order resource selection) [69, 70]. We delineated the resource units available to mule deer at the landscape scale by pooling all location data per study site and performing a minimum convex polygon (MCP) around all collected location data. We buffered these MCPs by the upper third quartile step length (945 m) for all individuals to prevent exclusion of space that was available to study animals beyond the outermost used locations [71, 72]. We randomly generated locations within each site's respective availability polygon. The ratio of used to available locations can heavily bias point-process models such as RSFs [73, 74]. To determine the appropriate number of available locations in each study site, we first gathered resource layers representative of distance to each land cover type for each crop-growing season for each study site (winter and summer; detailed above). We then sequentially sampled up to 100,000 random locations for each study site's availability polygon and compared the true mean of each layer to the calculated mean of each covariate under varying sampling intensities [75, 76]. For all covariates and sites, ≥ 25,000 random locations converged on the true mean of availability at the landscape scale. Thus, we paired each individual's monthly used locations with 25,000 random locations per month.

Prior to assessing the influence of cover type or crop availability of mule deer spatial ecology, we first tested how other landscape variables may influence resource selection between our selected study sites. We first pooled all data within each study site. For each individual within each site, we then fit a generalized linear model with a binomial error structure to assess how elevation, slope, terrain ruggedness, and distance to roads predicted probability of use. Site-specific population level selection was then calculated by averaging individual selection coefficients and calculating 95% confidence intervals.

To assess how land cover influences mule deer spatial ecology, we extracted distance to each cover type to each individual's set of used and random locations for each month. Using distance-based layers for land cover type within a RSF framework avoids mis-categorization of a collected GPS location (e.g., collar error), aids in identifying the use of edge habitat, and mitigates the effect of an individual using a land cover type in between collection of GPS locations (i.e., an individual foraging in cropland for 1.5 h in between 2-hour collection intervals) [77]. Individuals that were monitored for less than half of the month were excluded from the respective month. We pooled all data to run monthly RSFs including our covariates of interest; distance to shrubland, grassland, wooded, fallow fields, and cropland. We quantified monthly resource selection by fitting mixed-effect logistic regression models under a use-availability design using the "lme4" package in R v4.1.1 [70, 78, 79]. We fit models with a binomial error structure and a logit link [76, 80]. We used a random intercept for each individual and study site to account for the unequal sample size among individuals and sites [80]. We modeled resource selection independently for each combination of sex and month, resulting in 24 models.

To assess behavioral decisions regarding land cover use within monthly home ranges (3rd order) [69], we modeled resource selection using step selection functions (SSFs) at the population level [81, 82]. Using the same availability dataset generated for functional response modeling detailed above, we compared 15 available steps to each used step in each case-control setting [82]. Each case of used and available steps was used to extract resource attributes at the end of each step in their respective month and excluded individuals that did not have > 50% of potential GPS locations. We fit our population level SSF models with the same aforementioned variables from our RSF analysis using conditional logistic regression using the "amt" package in R v4.1.1 [83] and modeled step selection independently for each combination of sex and month, resulting in 24 models.

Individual-based step selection

SSFs use a case-control design to address issues with varying spatio-temporal availability of resources, such as varying crop species availability. Thus, we evaluated each crop species independently as covariates in our SSFs as opposed to a pooled "cropland" covariate. We fit monthly global SSFs for each individual to account for variation in crop species availability each deer experienced [84, 85]. To focus on crop-specific selection, we excluded individuals that never used cropland or occupied areas greater than the non-use threshold identified in our functional response modeling outlined above. We additionally catered each individual's model to the crop species that were available to them within their respective site for each monthly model. Because of the sensitivity to bias at the individual level [82], we employed a more strict exclusion of individuals that had < 80% of data within their monthly model respectively. Our modeling efforts totaled 1,074 individually based SSF models. We then averaged individual level coefficient estimates per month and sex to obtain population-level inference of crop species selection [86].

Lastly, we tallied the proportion of our individuals that selected or avoided a given crop type and compared these results to simple use metrics per crop species, sex, and month combination. Proportional use was calculated for individuals that occupied areas < 4.23 km from cropland (to compare to individual based SSF modeling). Crop species available to mule deer during the study were cotton, corn, winter wheat, alfalfa, sorghum, potatoes, and canola (listed in order of decreasing prevalence). Winter wheat and alfalfa were the only crops available during the winter growing season.

Prior to fitting all models, we examined multicollinearity for all covariates. No covariates were highly correlated ($r < 0.7$) and thus all were included in our modeling procedures. We also examined Variance Inflation Factor (VIF) for each fitted model and no population-based model exhibited a variable with a VIF > 5. Within the individual-based SSF modeling procedure; if a VIF > 5 was observed for a given variable, that individual's respective month-model of coefficient estimates were excluded from population averages.

Results

We captured, collared, and monitored 77 adult (> 1 year old) female and 69 adult male mule deer in the Texas Panhandle from 2015 to 2019. Our data set totaled 480,212 GPS locations for females and 353,510 locations for males, where each individual had a mean of 345 locations (SD = 53.5) per month. Mean home range size was 4,083.4 ha (*SD* = 3906.3) for males and 1,073.5 ha (*SD* = 701.0) for females (Fig. 2A; Additional File 5). The average proportion of a home range encompassed by cropland was 12.2% with a range of 0–68.1%. Within the home range (via generated availability for step-selection functions), mean proportion of available cropland was 10.8% with range of 0–47.2%.

Functional responses to cropland

Proportional cropland use was negatively influenced by home range distance to cropland. Our piecewise regression indicated breaks at 1.58 km (SE = 0.21) and 4.23 km (SE = 0.99); where cropland use was greatest at home range distance < 1.58 km from cropland, moderate or low from 1.58 to 4.23 km, and negligible at > 4.23 km (Fig. 2B). The coefficient for the first linear segment (closest to cropland) indicated a 13% decrease in proportional cropland use for every 1 km further from crops ($\widehat{\beta}$ = -0.1302, 95% CI= -1.632 ‑ -0.0971), a 2% decrease per 1 km in the second segment ($\widehat{\beta}$ = -0.0213, 95% CI= -0.04217 ‑ -0.0004), while the third segment demonstrated no relationship and no proportional use of cropland ($\widehat{\beta}$ = -0.00008, 95% CI= -0.0051 ‑ 0.00493; Fig. 2B). Our assessment of functional responses in habitat selection revealed decreasing curvilinear responses at multiple scales. When comparing availability of cropland at the home range scale to proportional use, a second order polynomial best described our data ($R^2 = 0.78$; Fig. 2C). Further, piecewise regression indicated that use was equivalent to availability within the home range ($\widehat{\beta}$ = 1.0265, 95% CI = 0.8710 ‑ 1.1824) until the home range comprised of more than 19.4% (SD = 1.8) cropland. Thereafter, decreasing use relative to availability (below 1:1 line) is observed ($\widehat{\beta}$ = 0.1129, 95% CI= -0.0043 ‑ 0.2301; Fig. 2D). Functional response at the within home range scale was also best described by a second order polynomial ($R^2 = 0.93$; Fig. 2E). Within home range piecewise regression indicated that use was nearly equivalent to availability ($\widehat{\beta}$ = 0.9277, 95% CI= 0.8640 ‑ 0.9914) until availability comprised of more than 23.4% (SD = 1.7) cropland. Thereafter, decreasing use relative to availability (below 1:1 line) is observed ($\widehat{\beta}$ = 0.3716, 95% CI= 0.2107 ‑ 0.5325; Fig. 2F). Both scales of analyses suggest mule deer use of croplands dropped below what was available when ~ 20% of the landscape is cropland.

Population-based resource and step selection

Our initial tests of resource selection relative to landscape variables beyond land cover types revealed little variation between our study sites. Site-specific population-level selection did not differ between sites for distance to roads and slope (Additional File 6). Moderate differences between sites existed relative to elevation and terrain ruggedness, however, the magnitude of these effects was not biologically substantial relative to relationships identified with land cover type (below; Additional File 6).

Our landscape scale RSFs (2nd order selection) revealed variation in preferred land cover type at the landscape scale dependent on the time of year. Females selected areas closer to cropland during January–March and July–August and males selected areas closer to cropland January–March, July–August, and October–November (Fig. 3A). Males selected areas closer to fallow fields inversely to cropland selection where these areas were selected April–June and September, months when areas near cropland was avoided (Fig. 3A). Females avoided areas near fallow fields (though still exhibited an inverse pattern to cropland selection; Fig. 3A), grassland, and wooded areas during most of the year (Fig. 3A). Males generally avoided areas near wooded areas and grassland during most times of the year apart from grassland during January–March (Fig. 3A). Both sexes selected areas near shrubland in all months.

Our population level step selection modeling (3rd order selection) had similar trends as the population level landscape scale models (2nd order selection). Males moderately selected for areas near cropland during December–February and females strongly selected areas near cropland during November–February (Fig. 3B). Interestingly, we also observed an inverse relationship with CRP or fallow field selection; where, during months when cropland was moderately avoided these areas were moderately selected (Fig. 3B). Females selected for areas near shrubland during nearly all months while grassland and wooded areas showed no pattern (Fig. 3B). Males generally selected for areas near shrubland and grassland from December–June with no generalizable pattern in subsequent months (Fig. 3B). Confidence intervals indicated a high degree of heterogeneity in selection patterns, likely due to individual differences in preferred cover types (see below).

Individual-based step selection

Our individual-based step selection modeling (for specific crop species) only included individuals that occupied areas < 4.23 km from cropland (*n* = 105), as indicated by the second breakpoint in distance-based functional response modeling above. We observed a high degree of individual heterogeneity. When averaging all individual selection coefficients to obtain population level inference, few generalizable patterns emerged (Additional file 7). Nonetheless, the proportion of individuals that selected alfalfa (8–60%), corn (17–86%), cotton (4–29%), fallow fields (8–52%), and winter wheat (9–63%) was highly time dependent (Fig. 4A). Furthermore, peaks in

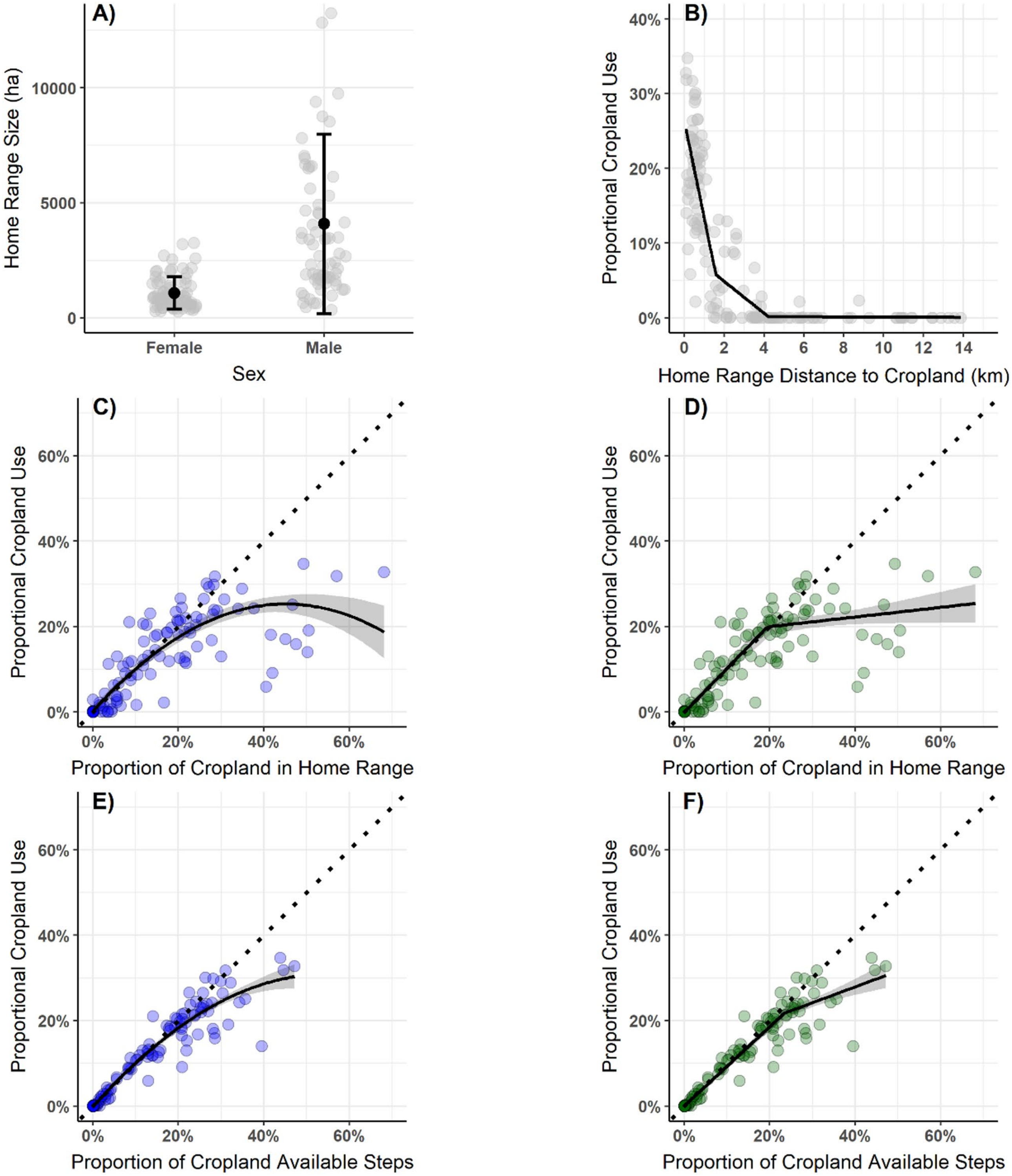

Fig. 2 Average home range size of 146 mule deer in the southern Great Plains from 2015–2019 (**A**) and the relationship between cropland use and average distance of the home range from cropland (**B**). Mule deer in this system display a functional response of use based on cropland availability at both the home range scale (**C** & **D**) and within home range scale (**E** & **F**; Available steps generated for step-selection functions). **B** indicates a piecewise regression to identify breaks in cropland use based on distance classes from cropland. **C** and **E** were fitted with a second-order polynomial regression and **D** and **F** were fitted with a piecewise regression to identify the point of deviation from a proportional linear relationship (dashed black line) between use and availability

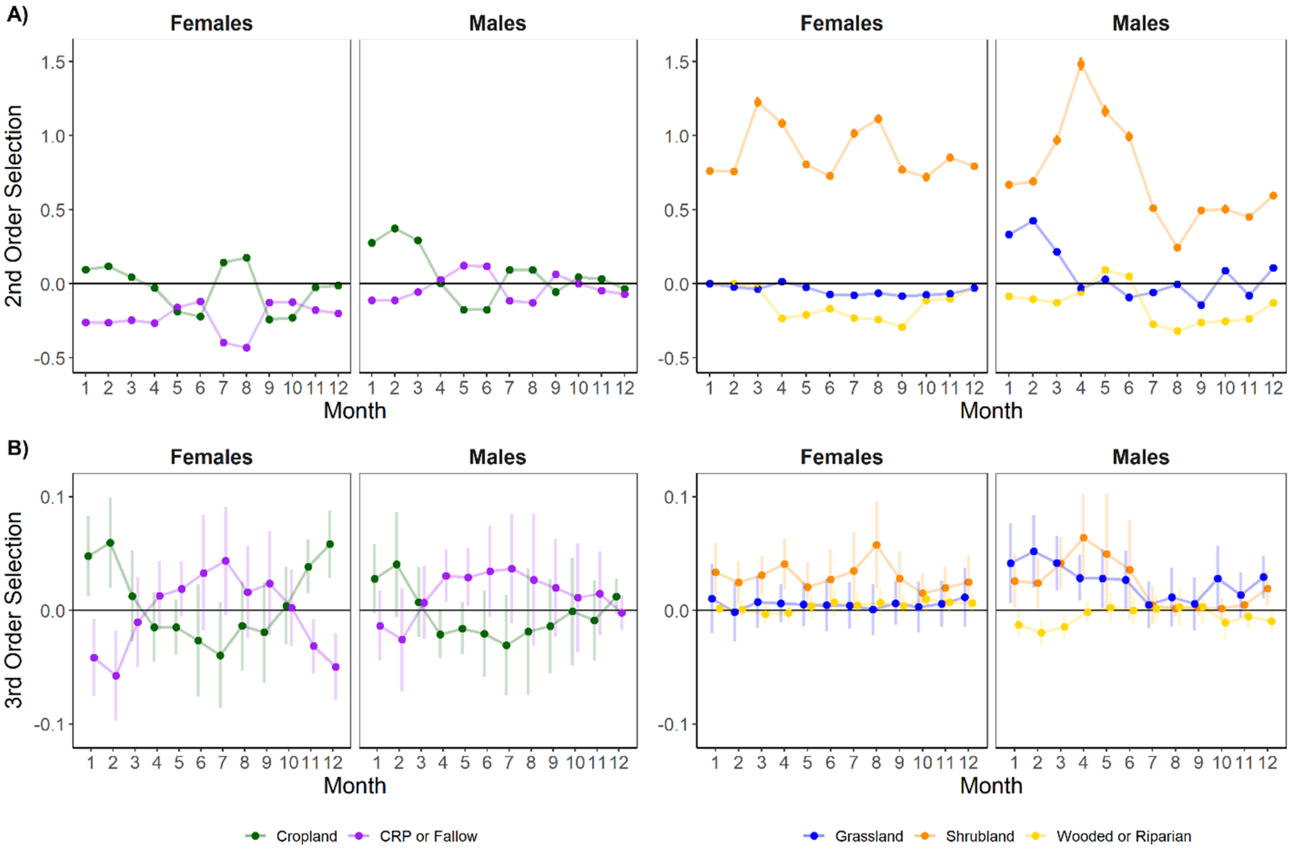

Fig. 3 Inversed selection coefficients from distance variables and 95% confidence intervals per month and sex from population level resource selection modeling at landscape scale (**A**) and step-selection selection modeling at the within home range scale (**B**). The horizontal black line indicates no effect whereas above the line indicates selection and below the line avoidance of the resource relative to availability. Conservation Reserve Program (CRP) or Fallow indicates fields enrolled in CRP or were dormant with native vegetation regrowth

selection were observed where ≥45% of the population selected alfalfa (March, April, July, and October), corn (July–September), and winter wheat (February–March; Fig. 4A). In general, the proportion of individuals selecting fallow fields was ≥25% most of the year.

Observed crop species use

Proportional use of cropland (not considering availability) varied highly among crop species (Fig. 4B). Generally, observed use of alfalfa and winter wheat was greater during September–December and January–March, respectively. Summer crop species (cotton and corn) had low proportional use except for later growth stages during August and September (Fig. 4B). Lastly, mule deer exhibited a moderate amount of time in fallow fields with a slight increase during the early summer months of May–July (Fig. 4B). Mean proportional use was negligible for potatoes (0.4%), peanuts (0.9%), canola (1.9%), and sorghum (6.1%); though, these crops were infrequent in our study system.

Discussion

As the human population increases, demand for food, textiles, renewable energy, and fossil fuels continues to rise. The Great Plains fill many of these demands, resulting in greater habitat heterogeneity for wildlife. Understanding anthropogenic influences on wildlife in this region will become increasingly important moving forward. Here, we demonstrate how row-crop farming alters the spatial ecology of a species in the southern Great Plains. There are only a few instances where row-crop dominated landscapes coincide with the mule deer geographic range, thus our knowledge of the influence of row-crop farming on mule deer is limited. In the face of a rapidly depleting aquifer that supplies all the irrigation to row-crop farming in the Texas Panhandle, we show that cropland presence and availability on the landscape alters spatial behavior of mule deer at several spatio-temporal scales. Seasonal cropland selection identified here corroborate previous findings linking mule deer population dynamics with cropland presence [27]. Though cropland may provide forage benefits, we demonstrate a threshold beyond which cropland becomes too abundant to sustain use of the resource (Fig. 2).

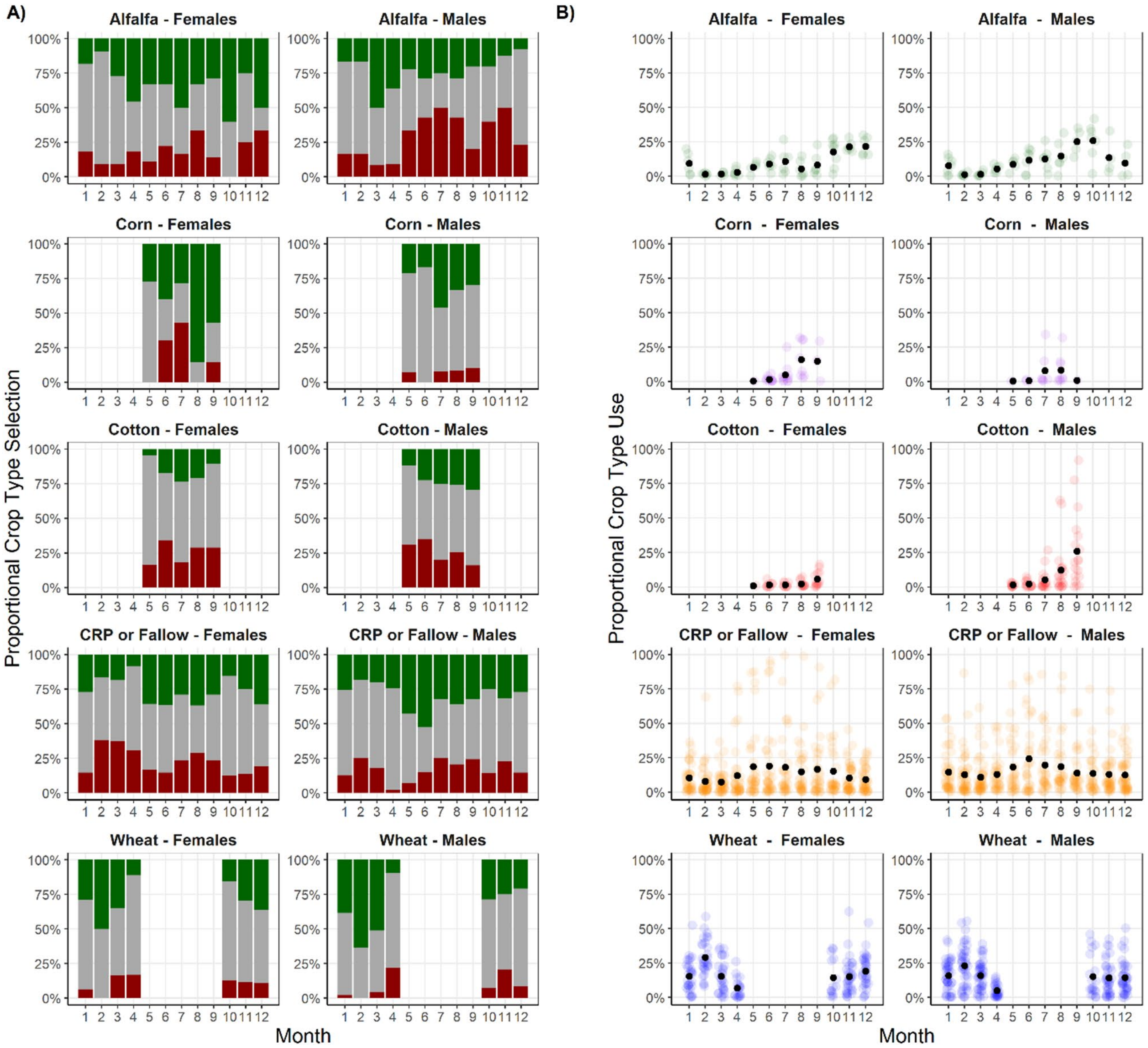

Fig. 4 (**A**) Proportion of individuals that select (green), avoid (red), or show no effect (gray) of specific cropland types based on individual based step selection modeling. (**B**) Proportional use of major crop types observed in our study by mule deer per month. Black points represent population averages. Proportional use is roughly equivalent to the proportion of time spent in each cover type. Both selection and use results represent only individuals that occupied areas < 4.23 km from cropland. Females are the left column and males are the right column, respectively. Winter wheat was only available October through April, corn and cotton were available May through September, and alfalfa was available year-round. Conservation Reserve Program (CRP) or Fallow indicates fields enrolled in CRP or were dormant with native vegetation regrowth

Our prediction that greater cropland coverage would limit cropland use was supported. Though row-crops may provide nutritional subsidies and are selected for seasonally, there is indeed a threshold beyond which use of cropland diminishes with increasing cropland coverage on the landscape for mule deer in the southern Great Plains. Specifically, proportional use diminished as the landscape coverage of cropland exceeded 20% at the scale of a mule deer home range and within home range movement. Further, no mule deer home ranges exceeded 68.1% cropland (mean = 12.2%) and generated available movement steps never surpassed 47.2% (mean = 10.7%), demonstrating that landscapes dominated by cropland deter mule deer occurrence. These findings are similar to other cervids, such as elk (*Cervus canadensis*), where row-crop use or selection is greater at lower densities of cropland [25]. Despite greater cropland coverage limiting cropland use, mule deer are attracted to row-crops during certain timeframes as they provide a means of enhanced nutrition relative to native forage sources [27]. We show, however, that individuals occupying areas further from cropland are unwilling to travel long distances

(> 4.23 km) to acquire this potential source of enhanced nutrition. Home range familiarity, perceived predation risk, or exhausting energy during travel to cropland may play a role in a risk-reward trade-off for mule deer [87, 88]. The native rangeland-cropland mosaic in the southern Great Plains will likely shift in the near future. Increasing food and fiber demands from a growing human population, juxtaposed by a decreasing aquifer provides a level of uncertainty to future land cover regimes. Conservation and management actions relative to these land cover limitations are paramount in understanding species' relationships with the environment [89, 90].

Based on our results, cropland coverage may be a contributor towards limiting mule deer range expansion eastward. We conducted our study at the southeastern fringe of the mule deer geographical distribution and in an area where highly prevalent cropland and mule deer coincide, unlike many other regions where mule deer are found. Despite some seasonal selection of cropland, our results begin to demonstrate that greater densities of row-crop farming limit use by mule deer at several spatial scales. Species range limits are often dictated by factors including climate, vegetation communities, topography, or anthropogenic influence [91]. In the United States, large mammal distributions and biodiversity are not uniform [92, 93]. Many of the native ungulates in the western United States are tied to mountainous terrain and their range expansion eastward is limited by differing vegetation communities and the lack of topography. Mule deer occupy the mountains and forests of the western United States; however, they also prefer open environments [38, 39]. For instance, Wiggers and Beasom [94] found that increased woody canopy cover was the main limiting factor defining the range limits of mule deer versus their counterpart, white-tailed deer, where their ranges overlap. When moving northward along the fringe of mule deer distribution (the Great Plains), however, woody canopy cover is not a defined barrier preventing eastward expansion. Our study sites were in the southern Great Plains, where greater woody canopy cover may similarly contribute as a limiting factor to mule deer geographic limits [94]. Moreover, we pose that cropland may influence the geographical distribution of mule deer [95], where increased cropland coverage (possibly at grander scales than we assessed) may be limiting eastward expansion.

A common row-crop farming practice in the Texas Panhandle is the use of winter wheat as a cover crop to provide forage to cattle and diminish erosion. Winter wheat in early phenological stages has a higher concentration of crude protein and digestible dry matter compared to many of the available native forage species in the region during winter [96]. At a population level, we observed strong landscape scale selection of cropland from January–March and moderate within-home range selection from January–February for male and females. Mule deer are likely selecting crop fields during winter because of the enhanced nutrition relative to the native rangeland [96]. Female mule deer are typically at the early stages of pregnancy during winter which has a relatively lower energetic demand compared to other stages of the reproductive cycle (i.e., late gestation and lactation) [97]. Acquiring energy stores to maintain body condition during winter may benefit females by preparing them for the energetically costly reproductive periods of late spring and summer; potentially a form of capital investment strategy [27]. Furthermore, rangeland conditions are poor during winter and females' protein requirements for developing young are increasing. Previous research has documented the importance of gestational nutrition on reproductive attempts by female mule deer [98–100]; where individuals that maintain greater body condition are more likely to successfully recruit young into the population [101]. Cropland, when coverage remains ≤ 20%, may serve as a forage source to elevate the nutritional plane of females in meeting these demands [27]. When above 20% coverage, however, our results demonstrate cropland may become a limiting landscape factor.

During the reproductive season (i.e., rut), male cervids reduce time spent foraging during the rut and may lose up to 40% of their body mass because of reduced energy intake and elevated energy expenditure while searching for and tending potential mates [102–104]. At the within-home range scale, females strongly increased cropland selection from November–December while males only displayed a mild within-home range scale trend towards selection in December. Peak conception and rut dates are in December in our study region [105]. Females may be selecting cropland during this time to prepare for gestation or recover from previous lactation [27]; likely because cropland has greater nutritional value compared to the native landscape [96]. Males, however, focus energy expenditure on mate-search and not nutrient acquisition during the rut. The strong within-home range scale selection of cropland by females in December results in a congregation of potential mates and therefore explains the increase in within-home range scale selection by males. The energetic deficit induced by reproduction facilitates a necessity for males to recover and maintain endogenous stores before the following year's mating attempts. Moderate selection by males for cropland (landscape scale) in the months leading up to rut indicates a shift of monthly space use closer to cropland and building up endogenous reserves before the energetically taxing reproductive season. Further, we show that male mule deer shift space use closer to cropland towards the final stages of rut and the months immediately following (January–March). As the proportion of receptive females in the population diminishes, males may switch their search strategy to larger congregations of females on row-crop fields. As the rut nears the end, males may then access cropland to begin a nutritional maintenance strategy or to replenish energetic stores used during the rut.

Cropland may additionally serve as an important source of nutrition for males developing antlers during summer. During all times of the year at the landscape scale, females avoided areas near fallow fields. Males, however, selected fallow fields during May and June and then exhibited a selection switch towards active cropland during July and August. This behavior may indicate that fallow fields act as a source of green-up in late spring, a time when males are undergoing antlerogenesis. As springtime forbs and overall nutrition diminishes in these areas [96], males then switch to active cropland where summertime species (e.g., corn, cotton) are at a later phenological growth stage and is accessible. Nutritional requirements change during antler development for male cervids [106]. Further, antler growth is directly tied to nutrient intake of individual males [106–108], and can enhance a male's competitive ability and reproductive success in a population [108–110]. The unique pattern of selection shift between fallow fields and active cropland may therefore be an indicator that cropland plays a role in nutrient acquisition for this crucial stage in male antler development. Interestingly, this inverse relationship of selection and avoidance between active cropland and fallow fields seems to hold true for all months between sexes and at the landscape and within-home range scale at the population level. These results suggest fallow fields may benefit mule deer during some seasons in the southern Great Plains, a finding that deserves additional research.

Inference from our results was indeed scale dependent. When assessing crop species selection at the individual level at the within-home range scale (3rd order), few generalizable patterns were observed across our sampled population. Furthermore, confidence in our estimates seems to vary substantially within our population level within-home range scale. The discrepancy between observed patterns at the landscape scale RSF versus the population and individual level within-home range scale SSF modeling highlights the processes that may shape mule deer movement. At the landscape scale, mule deer made broader monthly shifts in space use, likely to accommodate changes in native and cropland plant phenology. Once these broad scale movements are made, population averaged estimates (individual level selection coefficient means) indicate mule deer generally used cropland and rangeland in proportion to what is available. Furthermore, individual heterogeneity in resource selection is often documented and is an important aspect of understanding the spatial ecology of species at various spatiotemporal scales [72, 111]. By focusing on population level selection for a particular land cover type, individual behavioral patterns may be overlooked. Though our population means for cropland selection via individual level SSFs failed to detect selection or avoidance, we observed a differential pattern of selection when summarizing the proportion of individuals that selected or avoided various crop species. For instance, up to 63% of our population that occurred in areas near cropland selected winter wheat at the within-home range scale between January and March, similar to the population level pattern that was observed at our landscape scale RSFs. Furthermore, an increase in the proportion of individuals selecting corn and cotton during July and August may indicate the moderate selection patterns we observed at the landscape scale during the summer months. Even though our individual level SSF modeling did not provide generalizable population patterns for specific crop species, several of our observations suggest which crops may be driving selection at the individual level within home ranges by mule deer in this region.

Little research has been conducted specifically addressing mule deer spatial ecology relative to cropland, as there are few instances where extensive row-crop farming coincides with the mule deer geographic distribution. The increasing presence of cropland in the Great Plains and western United States makes such research important for mule deer conservation. Previous studies have documented broad scale cropland selection by mule deer; where cropland coverage decreased through time, however, mule deer selected the resource as it became less common [26]. We show a similar pattern where cropland use was greater relative to availability at lower cropland densities. Further, Carrollo et al. [46] identified seasonal selection of cultivated sunflowers (*Helianthus spp.*) in southwestern Colorado by mule deer. Though we did not have cultivated sunflowers in our study sites, we also show selection of particular crop species can shift seasonally, demonstrating that cropland is an important forage source for mule deer [27]. Alfalfa was not abundant in our system, however, of the individuals with access to it, a large proportion selected the resource much of the year. Carrollo et al. [46] demonstrated similar findings, where both diurnal and nocturnal selection of alfalfa seemingly shaped the spatial ecology of mule deer in their system. Large herbivores are inherently reliant on land cover and forage sources in their environments. Cropland may play a large role in shaping the spatial ecology and population performance of mule deer in these systems [27].

Conclusions

In areas dominated by row-crop farming, species are faced with an array of anthropogenic influences. As the human population continues to increase, demands for livestock production and farming will follow suit. These demands will likely modify croplands both in coverage and extent in the future. Our research demonstrates a threshold at which cropland coverage negatively influences occurrence of a prominent large mammal species in the Great Plains. Areas of > 20% cropland at the home range scale limit mule deer occurrence which can aid in understanding population dynamics and guiding future conservation or management actions of the species. Further, we show cropland areas, which are relatively unique throughout the mule deer geographic range, alter temporal trends in the spatial ecology of the species and at moderate or low densities may provide a nutritional subsidy. Changing climate and ground water depletion provides further complexities towards predicting future landscape change in these ecosystems. Despite increased demands in agriculture production, climate and ground water factors may limit row-crop farming with downstream effects on mule deer population performance [27].

Our population measures provide a baseline to produce an adaptive management plan for mule deer in the Texas Panhandle, as well as the southern Great Plains as rangeland-cropland juxtaposition continues to change. Additionally, as federal policy continues to shape cropland practices, our results will help state wildlife agencies adjust their survey methodology and harvest management for mule deer in a cropland-rangeland matrix. The rapid depletion of the Ogallala Aquifer only exacerbates the need to link landscape level factors with the management and performance of species occupying these regions, particularly in light of changing commodity production. Indeed, the combination of threatened water resources and an exponentially growing human population will likely shift row-crop farming practices in the future. Understanding the influence of human-induced changes on the landscape will further enhance the growing body of knowledge towards human-wildlife interactions and aid all stakeholders in understanding how these landscape linkages affect species within them.

Abbreviations

AIC	Akaike Information Criterion
AKDE	Autocorrelated kernel density estimator
CRP	Conservation Reserve Program
GPS	Global positioning system
MCP	Minimum convex polygon
RSF	Resource selection function
SSF	Step–selection function
VHF	Very high frequency
VIF	Variance inflation factor

Supplementary Information

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Supplementary Material 1

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Author contributions

D.G.H., R.W.D., T.E.F., L.A.H., W.C.C., and S.S.G. obtained funding and oversaw the project. L.J.H. and J.P.V. collected data for the project and L.J.H. analyzed the data. L.J.H. interpreted the results and wrote the manuscript with help from D.G.H. All authors provided editorial assistance.

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Data availability

The dataset supporting the conclusions of this article is available in the Movebank repository titled "Mule Deer Texas Panhandle", [https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study1916300396].

Declarations

Ethics approval and consent to participate

All animal capture and handling procedures were approved by the Institutional Animal Care and Use Committee at Texas A&M University-Kingsville protocol #2018-05-25 and were within guidelines established by the American Society of Mammalogists for research on wild mammals. We also complied with capture and handling procedures developed by the Texas Parks and Wildlife Department.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

Author details

[1]Caesar Kleberg Wildlife Research Institute, Texas A&M University – Kingsville, Kingsville, TX, USA
[2]Borderlands Research Institute, Sul Ross State University, Alpine, TX, USA
[3]Department of Natural Resources Management, Texas Tech University, Lubbock, TX, USA
[4]Texas Parks and Wildlife Department, Alpine, TX, USA
[5]700 University Blvd. MSC 218, Kingsville, TX 78363, USA
[6]Present address: Texas Parks and Wildlife Department, Hunt, TX, USA

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