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Original Article

Mark-Recapture Distance Sampling for Aerial Surveys of Ungulates on Rangelands

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ABSTRACT Aerial surveys are an efficient technique for counting animals over large geographic areas such as rangelands. In southwestern rangelands, aerial surveys are routinely conducted for ungulates, with the implicit understanding that abundance estimates represent an undercount. Distance sampling can correct for visibility bias, but assumes perfect detection on the survey line, a condition often violated in aerial surveys of ungulates. The incorporation of mark-resight methods into the distance-sampling framework, termed mark-recapture distance sampling (MRDS), corrects for both visibility bias and imperfect detection on the survey line. However, the use of MRDS introduces logistical and technical constraints that may not be practical for aerial surveys. We conducted aerial surveys of ungulates on rangelands in south Texas, USA, to evaluate the feasibility and performance of MRDS relative to conventional distance sampling (CDS) and multiple covariate distance sampling (MCDS). We conducted surveys prior to and after leaf-fall in 2013–2015 to test the hypothesis that distance sampling corrected for changes in visibility bias. We surveyed white-tailed deer (*Odocoileus virginianus*), nilgai (*Boselaphus tragocamelus*), collared peccary (*Pecari tajacu*), and feral swine (*Sus scrofa*) on 4 sites. Each site was surveyed seasonally for 2 years; twice both prior to (Nov) and after leaf-fall (Feb). Probability of detection on survey lines for each species was high (range = 0.82–0.97) and the average for each species was similar between seasons (0.89 and 0.92 during pre and post leaf-fall, respectively). The MRDS density estimates often were only ~10% greater than CDS and MCDS estimates; all population estimates had overlapping 95% confidence intervals. Further, CDS and MCDS estimates were similar indicating that measured covariates (seat position, vegetation type, and cluster size) contributed little towards detection probabilities. Despite similar average probability of detection for all species before and after leaf-fall (0.47 and 0.51, respectively), deer and nilgai population estimates were 22–59% lower during fall surveys than winter surveys. The discrepancy between consistent probability of detections with different population estimates suggests that availability bias, which cannot be addressed with distance sampling, was an issue. Overall, the MRDS technique addressed imperfect detection on the survey line and generated probabilities of detection in the survey area consistent with previous studies done in Texas. However, the extra costs (~US$13,000) and logistical hurdles to preserve observer independence for a small increase in precision of population estimates may not be justifiable.

KEY WORDS aerial survey, collared peccary, distance sampling, feral swine, mark-recapture, nilgai, rangelands, Texas, white-tailed deer.

Aerial surveys are one of the quicker ways to survey animals over large expanses of land or water (Caughley 1977, Cook and Jacobson 1979, Anderson and Lindzey 1996, Walter and Hone 2003). However, not all animals in the survey area are seen and population estimates derived from aerial surveys tend to be biased low (Caughley et al. 1976, DeYoung et al. 1989). Because animals farther off the survey line are less likely to be detected than animals closer to the survey line, visibility bias is a major cause of population underestimates. Conventional distance sampling (CDS) was developed to address visibility bias associated

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with unseen animals during surveys by generating a detection probability (p) as it relates to distance from the transect line (Buckland et al. 2001). The proportion of animals missed because of visibility bias can be estimated by $1 - p$. Thus, CDS relies on the assumption that 100% of animals on the transect line are seen, $g(0) = 1$. If the assumption is violated, counts are biased low by an unknown amount (White et al. 1989, Anderson and Lindzey 1996).

Distance sampling can be combined with mark-recapture methodology, an approach termed mark-recapture distance sampling (MRDS), to estimate detectability on the transect line (Buckland et al. 2004). If $g(0) < 1$, CDS population estimates can be adjusted (Buckland et al. 2004). Thus, the MRDS method can correct for the undercount found in aerial surveys by accounting for both decreased visibility with increasing distance from the survey line, and imperfect detection on the line (Pollock and Kendall 1987, Graham and Bell 1989, Marsh and Sinclair 1989, Southwell et al. 2002, Potvin and Breton 2005). The MRDS method has been used to account for visibility bias over a broad range of detection probabilities for aquatic and terrestrial animals, including cetaceans (Laake et al. 1997; Okamura et al. 2003; Cañadas et al. 2004; Southwell et al. 2007, 2008), kangaroos (*Macropus* spp., Fewster and Pople 2008) and brown bears (*Ursus arctos*, Walsh et al. 2010). Recent advances to MRDS also allow the inclusion and modeling of covariates such as vegetation cover or terrain (Borchers et al. 1998*a*, *b*).

Mark-recapture distance sampling offers a promising means to improve population estimates in situations where $g(0) < 1$. One such case involves rangelands in the southwestern United States, where aerial surveys are commonly employed to obtain population estimates of large mammals (Beasom 1979, DeYoung 1985, Beasom et al. 1986, Leon III et al. 1987, Shupe and Beasom 1987). Traditionally, aerial surveys of southwestern rangelands are conducted with fixed-width transects during autumn (Sep–Nov) because of the need to estimate population sizes prior to hunting seasons (Nov–Feb). Most autumn aerial surveys are conducted specifically for white-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*), with other native and exotic species also counted. Wildlife managers often prefer to conduct aerial surveys during February, after leaf-fall, because visibility bias appears to be which is thought to increase precision (Beasom et al. 1986). For instance, DeYoung (1985) found that uncorrected strip estimates were 36% vs 65% of mark-recapture estimates during September-November vs February, respectively.

Regardless of timing of surveys, previous studies have found high variation in the proportion of marked white-tailed deer (36–75%, DeYoung 1985, Beasom et al. 1986) and mule deer (19–77%; Zabransky et al. 2016) detected in replicate surveys. The among-survey variation in detection probability suggests that some deer were missed or not available to be seen during replicate surveys. DeYoung et al. (1989) proposed a fixed correction factor to correct strip transects for negative bias based on the relationship between proportion of animals missed and mark-resight estimates of collared deer. However, it is undesirable to rely on a fixed correction factor developed on only one site. Furthermore, 64% of variation in the correction factor was not explained by detection probability, which suggested ≥1 unmodeled variable influenced detections (DeYoung et al. 1989).

There is a need for a more accurate and precise survey method for large mammals in southwestern rangelands, especially as it relates to changes in visibility bias within or among years. The MRDS method appears promising, but requires additional technical and logistical considerations to preserve observer independence and track resightings. We evaluated the effectiveness and feasibility of the MRDS technique in rangelands. Although white-tailed deer are generally the focal species, there is little information regarding detectability for other ecologically and economically important rangeland ungulates, such as collared peccary (*Pecari tajacu*) and introduced exotics, such as nilgai antelope (*Boselaphus tragocamelus*) and feral swine (*Sus scrofa*). We conducted helicopter-based MRDS surveys on 4 sites in southern Texas, USA; each site was surveyed bi-annually for 2 years for the 4 target species. Bi-annual surveys occurred in autumn prior to leaf-fall, and in winter, after leaf-fall. In addition to MRDS, we also estimated population sizes via CDS and multiple covariate distance sampling (MCDS) for each species for each survey.

Our objectives were to: 1) evaluate the assumption of $g(0) = 1$ in southwestern rangelands; 2) assess whether distance sampling corrected for visibility bias between seasons (before and after leaf-fall); and 3) compare autumn MRDS estimates to a correction factor used for white-tailed deer during strip sampling (DeYoung et al. 1989). We predicted that: 1) MRDS would be an effective technique to use in rangelands, as indicated by high $g(0)$ and low CV (<20%) of density estimates; 2) species-specific population estimates would be similar among seasons (autumn and winter) after correction for visibility bias, given that annual birth pulses did not occur between seasons; and 3) autumn white-tailed deer population size estimates would be comparable between MRDS and the fixed correction method (DeYoung et al. 1989).

STUDY AREA

We conducted surveys on 4 ranches in southern Texas owned by the East Foundation. Specifically, we conducted surveys on the San Antonio Viejo, Buena Vista, El Sauz, and Santa Rosa ranches, which encompassed 81,616 ha of native Texas rangeland at ~1–180 m above sea level (Fig. 1). The vegetation consisted of Tamaulipan thornscrub (82%), which included honey mesquite (*Prosopis glandulosa*), prickly pear (*Opuntia* spp.), and granjeno (*Celtis pallida*). The remainder was open grassland (16%) and live oak (*Quercus virginianus*) woodland (2%). All ranches were surrounded by properties with similar land cover except for the eastern border of El Sauz, which bordered the Laguna Madre. Because all ranches were maintained as cattle ranches, all properties were contained by 1.2-m livestock fences. Portions of each ranch's boundary had

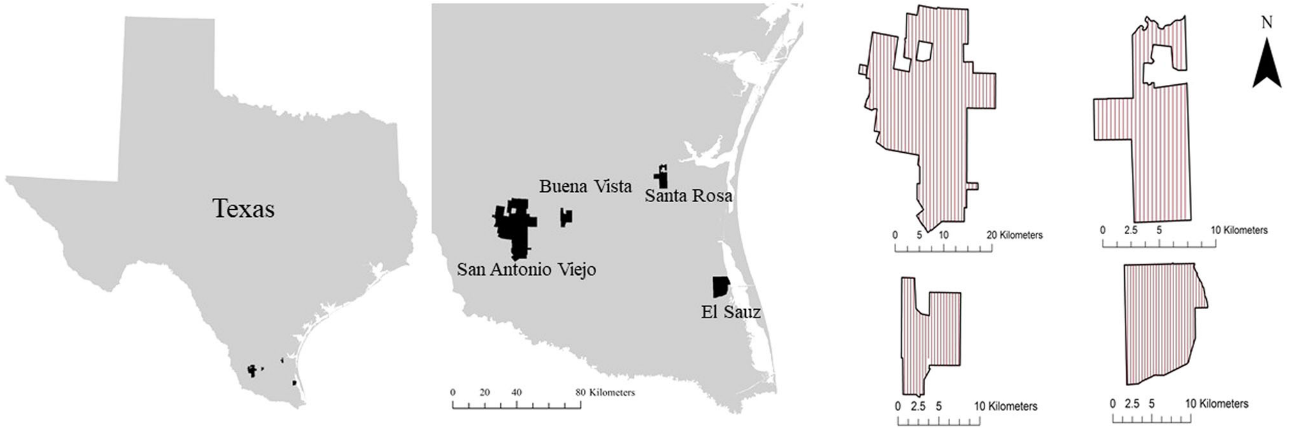

Figure 1. The location of our 4 study sites in south Texas, USA. We surveyed each site using distance sampling to count for white-tailed deer, nilgai, collared peccary, and feral swine during November 2013 to February 2015. Red vertical lines indicate survey transects.

fencing 2.5 m tall, but generally, wildlife species could enter and exit freely. Native white-tailed deer and collared peccary were present on all 4 ranches and were unhunted. Feral swine were present on all 4 ranches and removed opportunistically. Nilgai, an exotic antelope from India, have established populations only on El Sauz and Santa Rosa ranches. Nilgai were commercially hunted on El Sauz and about 35 male nilgai (~2% of total population) were harvested from January to March during both years of our study.

San Antonio Viejo (57,011 ha) was located 58 km southwest of Hebbronville, Texas, and spanned portions of 2 ecoregions: the Coastal Sand Plains and Texas-Tamaulipan Thornscrub (Griffith et al. 2007). Most of the ranch was composed of Tamaulipan thornscrub and grassland. Buena Vista (6,110 ha) was located 30 km southeast of Hebbronville, Texas. The ranch was within the Coastal Sand Plains ecoregion (Griffith et al. 2007) and dominated by a savannah of grasslands and widely spaced patches of woody vegetation. Santa Rosa (7,471 ha) was 20 km south of Kingsville, Texas, within the Coastal Sand Plains ecoregion. The southern portion of the property was closed woodland habitat dominated by live oak and the remainder consisted of Tamaulipan thornscrub. El Sauz (11,021 ha) bordered the Laguna Madre and was adjacent to Port Mansfield, Texas. It spanned portions of the Coastal Sand Plains, the Lower Rio Grande Valley, and the Laguna Madre Coastal Marshes ecoregions (Griffith et al. 2007). El Sauz was the most diverse in terms of vegetation communities relative to the other 3 properties. Closed-canopy live-oak woodlands dominated the northwest portion of the ranch, and the remaining area was grassland distributed within widely spaced patches of woody vegetation, wetlands, and expansive sand dunes.

METHODS

Aerial Survey Protocol

We conducted surveys during November 2013, February and November 2014, and February 2015; each ranch was flown once during each season. Target survey coverage was 50% (transects spaced every 400 m) on Buena Vista, Santa Rosa, and El Sauz and 25% (transects spaced every 800 m) on San Antonio Viejo. We based target coverages on expected ungulate densities for south Texas and, thus, expected encounter rates that would produce sufficient observations to conduct distance sampling analyses. The survey platform was a Robinson-R44 helicopter with the doors removed to increase visibility (Robinson Helicopter Company, Torrance, CA, USA). The helicopter carried 4 people; the pilot in the front right seat, an observer in the left front seat and 2 observers in the back seats. Prior to surveys, we loaded shapefiles of each ranch boundary and corresponding transects into a Garmin Nuvi-LM52 (Garmin International, Inc.) navigation unit, which the pilot used to follow the survey transects (Fig. 1). We flew systematic, evenly spaced transects on north-south azimuths created in ArcMap 9.3.1 (ESRI, Redlands, CA, USA), with a random starting location along a north or south border of the study site. The target flight altitude was 15 m above ground level and varied slightly (15–25 m) depending on vegetation and terrain (oak trees and sand dunes). The target flight speed ranged from 65–85 km per hr and fluctuated with the prevailing coastal winds.

In the context of MRDS with aerial surveys, animals seen by a single observer are considered marked, and if seen by a second, independent observer, are considered recaptured. Independence among observers is critical; thus, the observer and pilot in the front 2 seats were on a separate intercom system from those in the rear of the helicopter to ensure observer independence. Two Sigtronics SPA-4Si Dual Bus kits (Sigtronics Corporation, San Dimas, CA, USA) were wired to create independent intercom systems for each set of observers. All 4 observers were connected into a single system for communication outside of survey periods. We instructed all observers not to motion or point at an observation, as they could draw attention to animals that would otherwise not be seen by the other observer group. The front passenger and the pilot were considered Observer 1, and the 2 back passengers were considered Observer 2 for analysis purposes.

Excluding the pilot, observers recorded data in 2 different ways during the study. During November 2013, February 2014, and February 2015, we used a manual data recording system in which observers wrote data on paper datasheets. Each observer in the helicopter penciled in their own data and marked their own waypoints with handheld GPS units. The front observer recorded the pilot's observations. During November 2014, we used a customized application (CyberTracker software, CyberTracker Conservation, Cape Town, South Africa) on a portable touchscreen laptop to enter data. One Toughbook (Panasonic, Osaka, Japan) was controlled by the front passenger and one by a back passenger. When a detection was made, an observer pressed a button on the touchscreen interface, which generated a GPS waypoint and also recorded the verbalized observation. Audio tracks of each observation were recorded by PA-80H/Digital Audio Recorder Adapters (Pilot Communications, Irvine, CA, USA) that were fitted on the helicopter headsets. The GPS points were marked through the CyberTracker program using Garmin 18X USB GPS sensors (Garmin International, Inc.). We discontinued use of the Toughbook during February 2015 because the device would periodically freeze and the GPS connection was not reliable.

We scanned for animals ahead of, and on both sides of, the helicopter. Most animals responded to the helicopter; thus, we used the location of first detection as the point for estimating perpendicular distance. We recorded animals ≤100 m on either side of the transect line so that transects were 200 m wide. The observers estimated perpendicular distance in 10-m intervals when detection was off the transect line. Specifically, any detections 0–5 m from the transect line was considered to be on the line and then detections were assigned to 5–15 m, 15–25 m, and so on intervals out to 100 m from the helicopter. When a detection occurred, we recorded the perpendicular distance from the transect line, group size, and sex and age (adult or young of the year) of the animal(s). Sex classifications were not recorded for collared peccary and feral swine due to a lack of sex-specific physical characteristics visible from a distance. Perpendicular distances between location of animals when first seen and the transect were visually estimated, not measured with rangefinders, because the helicopter had to continue moving to preserve observer independence. If the helicopter were to stop and hover to measure a distance, or if observers could see another observer pointing a rangefinder, they would become aware that a detection had occurred, resulting in inflated recapture rates and violation of the assumption of observer independence.

Accuracy of Estimated Distances

Visual estimation introduces the possibility that bias or inaccuracy in distance measurements could affect population estimates. To mitigate for the bias or inaccuracies, we used 2 methods to calibrate observers prior to and during surveys. First, we built an array of metal posts placed at 20-m increments out to 100 m. The pilot flew by the posts at the beginning of the survey and each time the helicopter refueled so that observers could calibrate estimated distances when the helicopter was perpendicular to the posts. Second, while flying to the next transect, the helicopter would momentarily hover while the observers calibrated their distance measurements by using laser rangefinders (Leupold RX-1000i; Leupold Optics, Beaverton, OR, USA) at random objects (fence posts, trees, etc.). Total number of nonpilot observers for each season from November 2013 to February 2015 was 8, 9, 3, and 3, respectively. The same pilot flew all surveys.

When time allowed, we quantified observer accuracy from the ground by estimating distances to objects at distances unknown to the observers. Observers were instructed to estimate the distance to the object from a certain point. The actual distance to the object was measured once estimates were recorded.

Statistical Analysis

After completing surveys, we compared observations between observers in the front and back of the helicopter to determine whether they were single observations (marks) or matched observations (recaptures). We compared observations by reviewing data recorded for each observation (sex, species, distance, and cluster size) and comparing waypoint locations in ArcMap 9.3. Because vegetation communities can influence detection probabilities, each observation waypoint was assigned to a vegetation community type based on layers from the National Land Cover Database (www.mrlc.gov, accessed 15 Jan 2015). Vegetation communities were categorized as grassland, Tamaulipan thornscrub, or oak woodland. Terrain and animal activity were not considered as covariates that could influence detection probabilities because the terrain was relatively flat and very few detected animals were inactive.

We analyzed data using the MRDS Engine in Program Distance 7.3 (Thomas et al. 2010) that runs in conjunction with the MRDS package in Program R (Laake et al. 2015; R Version 3.3.2, www.r-project.org, accessed 2 Feb 2020). For each survey season (e.g., Nov 2013), we pooled data across all 4 ranches (2 ranches for nilgai) and fit a global detection function for each species. It is probable that detection probabilities vary for each ranch, but we wanted to focus on evaluating MRDS in southwestern rangelands as an ecoregion instead of being ranch-specific. For the mark-recapture component for all surveys, we used a generalized linear model with a logit link function.

It is recommended to obtain ≥60 detections among 10–15 transects to generate reliable estimates using the distance sampling method (Buckland et al. 2001, 2015). We combined detections of feral swine and collared peccary during each survey because there were insufficient detections to analyze each species separately (Buckland et al. 2001). The 2 species have similar physical characteristics (body size, locomotion, herd formation; Davis and Schmidly 1994); thus, their detection probability was expected to be comparable. For each season, we used the proportion of observations made for each species (e.g., 0.30 swine and 0.70 peccary) to estimate each species' density.

Model Selection

We truncated distance data at 95 m and increased the first distance bin from 0–5 m to 0–15 m to relax the frequently-spiked detection functions due to observers possibly rounding down to nearest distance interval (Buckland et al. 2015). We evaluated up to 13 models for each species, which included a null model in addition to each possible combination of one or 2 covariates including interactions. Covariates were vegetation type, seat (front or rear), seat position (front left, rear left, front right, or rear right), and cluster size. Seat position was not used as a covariate during the November 2014 surveys because there was insufficient time to record this information in the Toughbooks. All distance sampling models had a key function of half normal (Buckland et al. 2015, Gonzalez et al. 2017). We used the independent observer, point independence method for the mark-recapture model for all surveys, which reduces negative bias associated with sensitivity to unmodeled heterogeneity and requires fewer assumptions (Borchers et al. 2006). Although Burt et al. (2014) recommended the independent observer, full independence method when responsive animal movement is expected, our helicopter moved at speeds that results in little time for the animal to significantly move before being detected. The best supported model was selected based on Akaike's Information Criterion (AIC) value.

While MRDS was our focus, we also generated population estimates via CDS and MCDS to examine differences among estimators (Melville et al. 2008). For the CDS and MCDS estimates, we tested 6 models for each species: a null model (CDS) and all possible combinations of covariates (limited to 2 covariates per model without interactions). To maintain consistency with MRDS analyses, all models were limited to half-normal key functions (Gonzalez et al. 2017) with the model with the lowest AIC value among the 3 series expansions (cosine, hermite polynomial, and simple polynomial). Constraints were set at strictly monotonically (Gonzalez et al. 2017). The best supported model was selected based on AIC value, but occasionally the lowest AIC value was ignored in favor of other models when population estimates of the initially-selected model were implausible (Gonzalez et al. 2017).

We compared white-tailed deer population estimates derived from MRDS to a previously published technique that corrects for deer not seen (including not available) during aerial surveys in southern Texas rangelands (DeYoung et al. 1989). Only autumn MRDS estimates were used for comparision because the correction factor was developed for autumn surveys (DeYoung et al. 1989). DeYoung et al.'s (1989) correction factor equation states:

$$c = 2.0 + 0.02x$$

where c represents the correction factor and x represents the proportion of animals missed within the 200-m transect width. The x is usually unknown, therefore, to estimate the detection probability during the surveys, we used estimated p generated by MRDS and estimated x as $1-p$. For instance, if MRDS determined p to be 0.55, the correction factor $= 2.0 + (0.02 \times 0.45) = 2.9$. Then taking the total number of individual deer seen (e.g., 500) during a survey with 35% coverage, the estimated population size would be 4,143 deer ([2.9 correction factor × 500 deer]/0.35 survey coverage).

RESULTS

Accuracy of Estimated Distance

There was a linear relationship between estimated perpendicular distances and distance to known objects ($r = 0.90$, $P < 0.01$; Fig. 2). The relationship indicated an overestimate of 4.3 m for objects 20 m from the transect line and an underestimate of 3.7 m at 100 m. However, there was no relationship between estimation error and perpendicular distance ($r = 0.04$, $P = 0.18$; Fig. 2). Out of 44 distance estimations, 18 (41%) were ≤5 m of the actual distance, 22 (50%) were >5 m and ≤10 m of the actual distance, and only 4 (9%) were >10 but ≤20 m of the actual distance.

Data Collection

We experienced issues with GPS navigational equipment that resulted in departures from the targeted survey

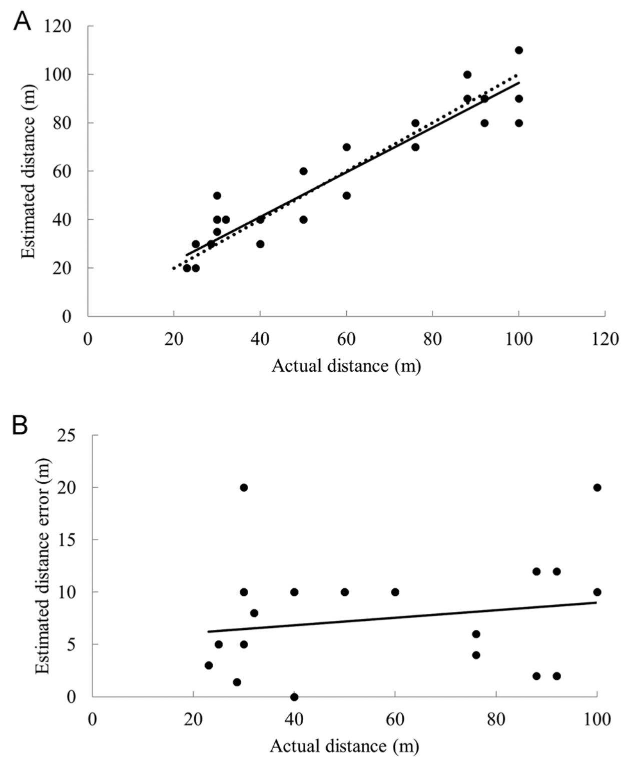

Figure 2. Linear relationship between A) estimated perpendicular distance measurements and actual distance measurements of stationary test objects and B) estimated perpendicular distance measurement error and actual perpendicular distance of stationary test objects during aerial surveys conducted for large mammals on East Foundation lands, Texas, USA, from November 2013 to February 2015. In panel A, the dashed line indicates a perfectly linear relationship whereas the solid line indicates the observed trendline. A total of 44 measurements were collected; some points with identical values are hidden.

coverages for some ranch-year combinations (Table S1, available online in Supporting Information). However, we were able to record >60 observations during each survey season for each species or species group (Table S2, available online in Supporting Information). Specifically, the number of animal clusters we detected during autumn 2013, winter 2014, autumn 2014 and winter 2015 was: 532, 749, 583, and 924 for white-tailed deer; 93, 184, 99, and 226 for nilgai; and 63, 156, 100, and 205 for collared peccary and feral swine. The proportion of observations made solely by the front or the back observers (marks) and observations seen by both (recaptures) varied among survey periods. For the November 2013 surveys, the front observers detected more marks (31%) than the back observers (25%). For the remaining surveys, the back observers saw more marks (27–31%) than the front observers (17–21%). The percentage of recaptures was lowest during the November 2013 surveys (44%) and remained at about 52–53% in subsequent surveys (Fig. S1, available online in Supporting Information). Transect-specific vegetation communities (200-m width) were consistent among survey seasons; 50% (range = 48–52%) were Tamaulipan thornscrub, 45% (range = 43–47%) were grassland, and 5% were oak woodland. Most animal detections occurred in Tamaulipan thornscrub, followed by grassland (Table S2, available online in Supporting Information).

Modeling Results

Detection function.—Frequency of detections declined with distance from the transect for each species during each survey (Fig. 3). Overall, cluster size was the most influential covariate; models including cluster size as a covariate were the top model for 11 of 12 season-specific surveys (Table S3, available online in Supporting Information). Several other season-species-specific models were <2.0 ΔAIC; however, population estimates were generally similar regardless of which covariate was included (Table S3, available online in Supporting Information).

Probability of detection.—The estimated proportion of animals seen on the line ranged from 0.82 to 0.97. White-tailed deer numerically had the largest average probability of detection on the line (0.94), followed by nilgai (0.91) and collared peccary-feral swine (0.89; Table 1, Table S4, available online in Supporting Information). Probabilities of detection on the line were numerically greater during February than November for 4 of the 6 species-specific seasonal surveys (Table 1). For white-tailed deer, $g(0)$ was 6% and 3% greater during post leaf-fall surveys relative to pre leaf-fall during the 2013–2014 and 2014–2015 seasons, respectively. Further, during the 2014–2015 surveys, $g(0)$ was 9% and 12% greater during February surveys for nilgai and feral swine-collared peccary, respectively.

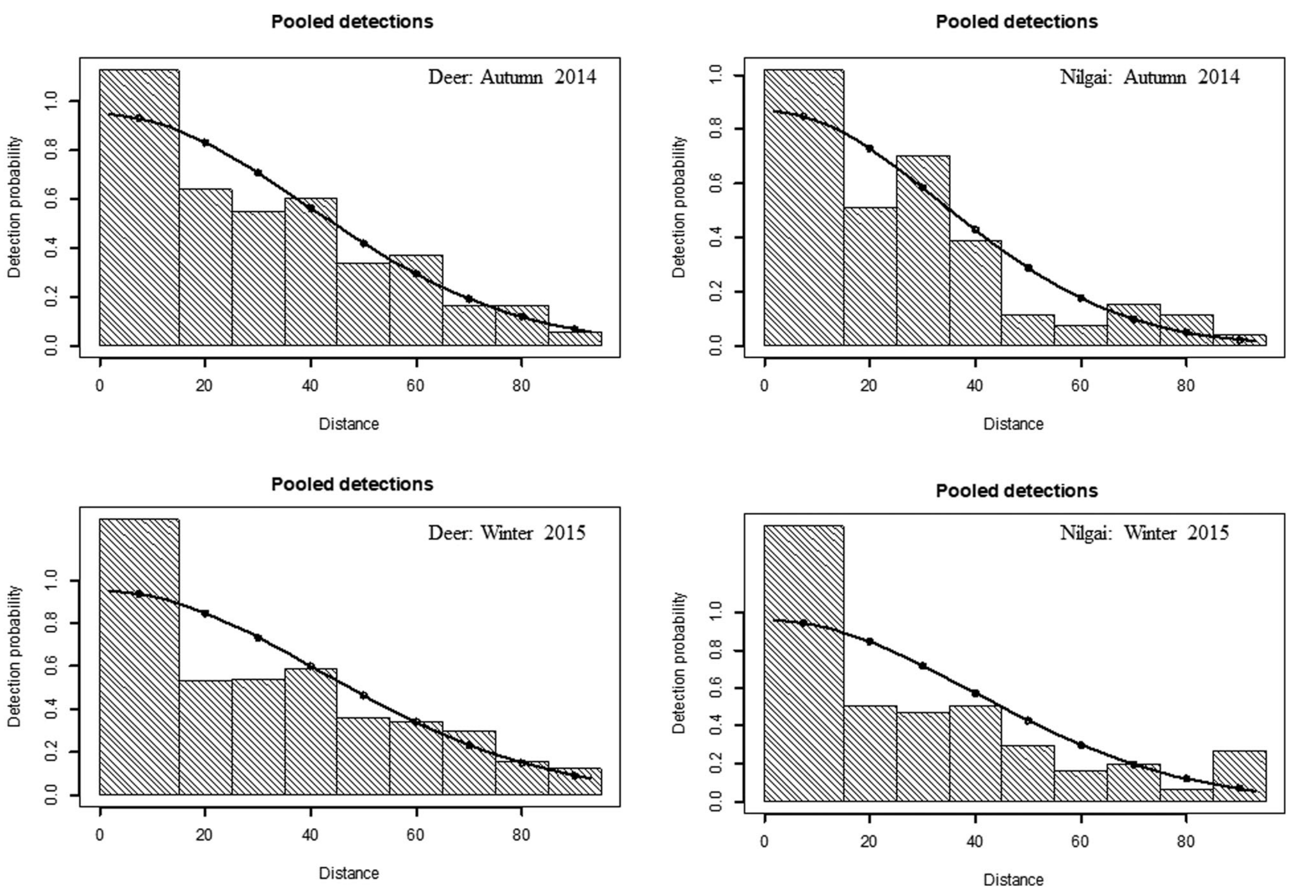

Figure 3. Detection probabilities for white-tailed deer and nilgai from mark-recapture distance sampling aerial surveys on East Foundation lands, Texas, USA, across 2 survey occasions (November 2014 and February 2015). Circles indicate detection probability for each observation.

Table 1. Probability of detection on the line, $g(0)$, detection probabilities (P), and effective strip width (ESW, m) by survey occasion for white-tailed deer and nilgai with associated standard errors (SE) and coefficients of variation (CV, %) during mark-recapture distance sampling (MRDS) aerial surveys for large mammals on East Foundation lands, Texas, USA, November 2013–February 2015.

Survey period	Species	$g(0)$	SE	CV	P	SE	CV	ESW
November 2013	White-tailed deer	0.91	0.02	2.2	0.55	0.02	4.2	52.3
	Nilgai	0.97	0.02	2.4	0.53	0.05	9.8	50.4
February 2014	White-tailed deer	0.97	0.01	0.1	0.65	0.02	2.9	61.8
	Nilgai	0.85	0.05	6.0	0.45	0.04	8.6	42.8
November 2014	White-tailed deer	0.92	0.03	2.9	0.47	0.02	4.4	44.7
	Nilgai	0.87	0.06	6.4	0.38	0.04	9.3	36.1
February 2015	White-tailed deer	0.95	0.01	0.9	0.51	0.01	2.8	48.5
	Nilgai	0.96	0.02	2.0	0.49	0.03	5.8	47.6

Overall, average detection probability for all species and seasons was 0.49 (range = 0.32–0.65; Table 1, Table S4, available online in Supporting Information). Average detection probability was numerically largest for deer (0.54), followed by nilgai (0.46) and collared peccary-feral swine (0.46). Trends in seasonal changes in detection probabilities were similar to what was observed with $g(0)$. Detection probabilities were numerically greater during February than November for 4 of the 6 species-specific seasonal surveys (Table 1, Table S4, available online in Supporting Information). For white-tailed deer, p was 15% and 8% greater during February surveys relative to November surveys for both years (Table 1). During the 2014–2015 survey, p was 22% and 37% greater during February surveys for nilgai and feral swine-collared peccary, respectively.

Density and population estimates.—Densities for deer and nilgai via MRDS were lower for autumn surveys than winter surveys (Fig. 4). Swine and peccary autumn densities were also lower than winter surveys in 2013–2014 (Fig. S2, available online in Supporting Information). The MRDS estimates for white-tailed deer were statistically lower during autumn 2014 than winter 2015 (non-overlapping 95% CIs). White-tailed deer density estimates were 22% and 31% lower during 2013–2014 and 2014–2015, respectively. The MRDS density estimates for nilgai were statistically larger during winter 2015 than autumn 2014 (non-overlapping 95% CIs); autumn estimates were 31% and 59% lower than winter estimates during 2013–2014 and 2014–2015, respectively. Feral swine and collared peccary density estimates were 31% greater during winter 2014 than autumn 2013, but the opposite occurred during the following season. During each survey occasion, more collared peccaries were observed than feral swine (Table S5, available online in Supporting Information). Density estimates for collared peccary were 54% greater during autumn 2013 than winter 2014 and vice versa during autumn 2014 and winter 2015. Feral swine densities were similar during the first 2 surveys and the last 2 surveys (Table S5, available online in Supporting Information). Overall, 10 of 12 density estimates had CV <20%; density

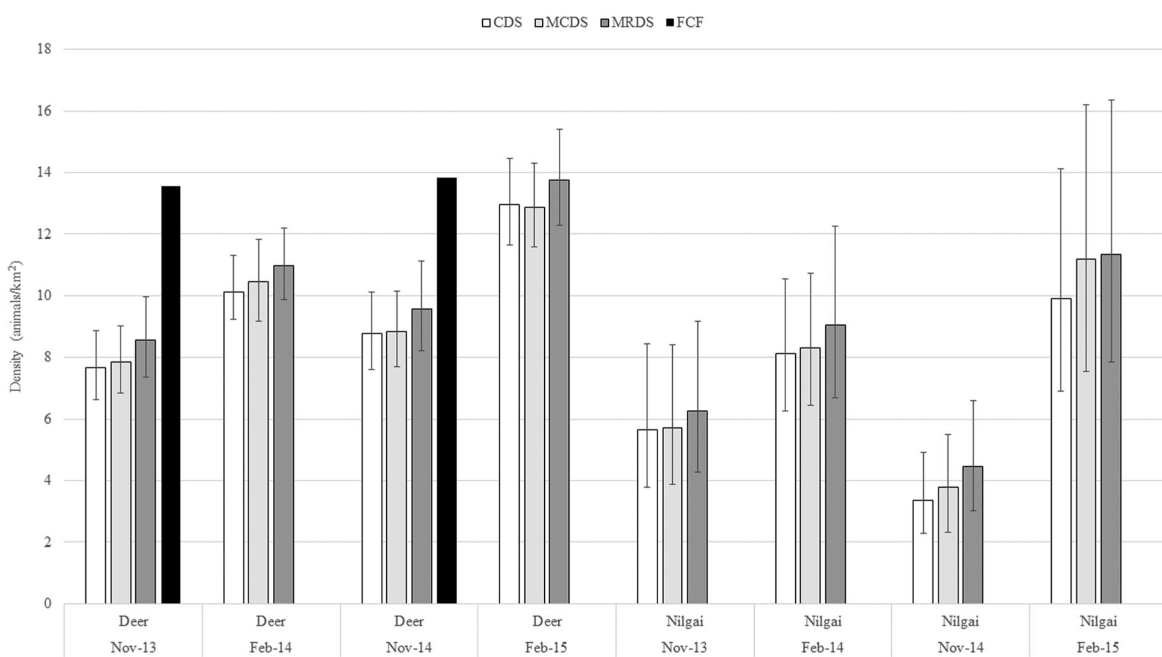

Figure 4. Density estimates (animals per km^2) for white-tailed deer and nilgai from aerial surveys on East Foundation lands, Texas, USA, across 4 survey occasions from November 2013 to February 2015. CDS = conventional distance sampling, MCDS = multiple covariate distance sampling, MRDS = mark-recapture distance sampling, FCF = fixed correction factor. Bars indicate 95% CIs.

estimates for white-tailed deer were relatively precise (CV range ≤ 5–7%), whereas estimates for nilgai (CV range = 12–20%) and collared peccary-feral swine (CV range = 13–22%) were more variable.

Relative to the MRDS estimates, CDS were underestimates for 10 of 12 season-species specific surveys; the underestimates averaged 12.8% (range = 4–33%; Fig. 4; Fig. S2, available online in Supporting Information). The 2 instances when CDS estimates were larger than MRDS occurred with collared peccary and swine; the average overestimate was 5% larger than MRDS. The most severe underestimates occurred during the autumn 2014 surveys for collared peccary and swine (26%) and autumn 2015 in nilgai (33%). The CDS estimates for white-tailed deer were consistent underestimates (6–12%) relative to MRDS. The addition of covariates to CDS (MCDS) resulted in negligible differences in densities; most MCDS estimates (10 of 12) were ≤3% of CDS estimates indicating that measured covariates did not have as strong effect. Further, 3 null MCDS were the favored model resulting in identical MCDS and CDS estimates (collared peccary and swine during the first 3 surveys). Despite CDS and MCDS frequently being underestimates relative to MRDS, 95% CIs overlapped for all 3 distance sampling methods for each season (Fig. 4; Fig. S2, available online in Supporting Information).

Our MRDS deer densities were lower than estimates generated by the correction factor during both autumns (Fig. 4; DeYoung et al. 1989). Specifically, November 2013 MRDS (n = 6,954, 95% CI = 5,973–8,096) was 39% lower than the estimated generated by the correction factor (n = 11,453). Similarly, during November 2014, MRDS (n = 7,777, 95% CI = 6,691–9,038) was 34% lower than the corrected estimate (n = 11,697).

DISCUSSION

Efficiency of MRDS in Rangelands

Mark-recapture distance sampling was successful in producing population estimates for all species for which we had an adequate number of detections. The average overall detection probabilities in the area surveyed for each of the 3 species ranged from 46 to 54%, indicating we saw about half of the animals in the survey area. Our detection probabilities estimates were greater compared with strip transects conducted in South Texas solely for white-tailed deer, where detection probabilities averaged 36% (DeYoung 1985, DeYoung et al. 1989). However, judging by the frequency of animals not marked by the front observer position compared with the rear observer position, greater detection probabilities relative to prior studies may have been expected given the additional observer during our surveys (versus 1 pilot and 2 observers; DeYoung 1985, DeYoung et al. 1989). Regardless, precision for detection probabilities in our surveys were comparatively high (CV range = 2.8–14.4%).

Using MRDS mitigates the assumption of CDS that all animals on the transect line are not detected by incorporating an estimate of the proportion of animals on the line that are detected. We found that MRDS frequently resulted in only a ~10% increase in the estimated white-tailed deer and nilgai population sizes relative to CDS and MCDS estimates. The lone outlier was from nilgai during November 2014 surveys; CDS and MCDS were 22–33% lower than MRDS estimates, which we suspect is from issues associated with the Toughbooks. Our suspicions are based on only 2 audio recorders being available during the November 2014 surveys, which may have contributed towards the relatively low average p for nilgai (0.38 vs. 0.49 during the other 3 surveys). The consistent ~10% underestimate during November 2013, February 2014, and February 2015 for white-tailed deer and nilgai is logical given the proportion of animals detected on the survey line was ~90%. Collared peccary and swine were more variable, which may be because of their relatively small body size, slow locomotive speeds, or low number of detections. Given that white-tailed deer and nilgai population estimates during February were frequently >10% larger than November estimates, the added difficulties and costs (~US$13,000; Table S6, available online in Supporting Information) of employing a double-observer method for a small increase in estimated population size may not be justifiable from a wildlife management perspective. Instead of using MRDS, CDS and MCDS may be a simpler, yet viable technique to survey wildlife in rangelands if the remaining assumptions are met.

The assumption that animals are fixed at the location they were initially sighted and none are counted twice could be violated if animals are running when first seen, animals are double counted, or when animal distribution is affected by the observer (Buckland et al. 2001). Because most animals were running when first observed during our surveys, animal movement in response to the helicopter could have biased our results. However, if animal movement is random and slower than the observer's speed, no serious bias occurs (Buckland et al. 2001). Animal movement that alters population estimates can occasionally be discovered by abnormalities in the detection function, such as a low number of detections on the transect line and a high number of detections at farther distances (Buckland et al. 2001). Because no significant abnormalities were detected in our models, biases associated with animal movement away from the transect line may not have had a meaningful effect on population estimates. Regardless, animal movement creates potential for double counting, especially with less space between transects (Buckland et al. 2001). There is little information on how far animals move as a response to helicopters, but the response probably differs as a result of animal behavior and vegetation community. Repeated surveys of collared mule deer counted using parallel transects similar to our study revealed that double counting occasionally occurred (Zabransky et al. 2016). However, collared deer movements in response to a helicopter also resulted in avoidance of detection in about 30% of surveys because deer moved in such a way that observers had no opportunity for detection (Zabransky et al. 2016). Foley et al. (2017) found that movement rates (150 m/hr) did not differ for nilgai the day before, during, and the day after helicopter surveys. In contrast, Linklater and Cameron (2002) found that all groups of feral horse (*Equus caballus*, $n = 17$) responded to a helicopter and moved an average of 1 km linear distance, including up to 2.75 km. The movement translated into a crossing of an average of 3.5 transects and up to 10 transects (Linklater and Cameron 2002). Similarly, 31% of feral goats (*Capra hircus*) moved up to 1.5 km during helicopter activities (Tracey and Fleming 2007). However, most of the feral goats moved between 150–325 m when within 100 m of the helicopter (Tracey and Fleming 2007), which would result in a minor double-counting issue with our smallest transect width (400 m). Given the tendency for white-tailed deer, collared peccary, and feral hogs to run towards the nearest cover as a response to the helicopter (A. Foley, unpublished data), double-counting is likely at most a minor issue except in open grasslands where cover may be at a considerable distance from the transect. Nilgai have a tendency to continue to run after being flushed (A. Foley, personal observation); thus, double-counting for nilgai could be an issue. The issue of double counting could be evaluated by using marked animals to observe drifting and adjusting the counts based on that information.

The last assumption relating to CDS is that all distances and angles are measured correctly. The results from our assessment of perpendicular distance estimates indicated that error in distance estimates in rangelands were small relative to size of distance bins, and errors did not increase with increasing distance from the transect line. Overall, we found no evidence that CDS assumptions were violated; thus, the use of CDS while accounting for covariates (MCDS) appear to be a viable approach to estimate ungulate population densities in rangelands (Southwell et al. 2007).

Seasonal Changes in Densities

White-tailed deer.—Unexpectedly, population estimates for white-tailed deer via all variants of distance sampling were lower in autumn versus winter. A population increase between autumn and winter surveys is difficult to explain because the reproduction pulse occurs during the summer months and therefore, reproduction cannot be the reason why the populations apparently increased. There are several possible reasons why deer populations appeared to increase between autumn and winter surveys. First, visibility of deer during surveys may have changed between survey periods because November is prior to leaf-fall and February is after leaf-fall. But if sightability of deer available to be seen changed, we would have found much larger detection probabilities and effective strip widths during post leaf-fall, which did not occur. Further, visibility may have changed because deer habitat selection could vary with seasons; however, vegetation community was not an important covariate in our models and proportion of detections in relation to vegetation communities did not change between seasons. Further, large shifts in distribution have not been documented for deer in South Texas as deer often exhibit high site fidelity (Webb et al. 2007, Hellickson et al. 2008). Because MRDS does not account for availability bias (animals unavailable to be seen), we hypothesize that differences in population estimates occurred because deer were less available to be seen during autumn surveys than winter surveys in this semi-arid and humid subtropical environment. Previous studies of aerial surveys in mule and white-tailed deer also suggested that availability varied among surveys within the same season (DeYoung et al. 1989, Zabransky et al. 2016). Availability bias is difficult to address without marked animals, though one might adjust survey protocols to mitigate for the bias. For instance, Melville et al. (2008) reported conducting surveys in subtropical portions of Australia only during morning and afternoon hours to minimize availability bias due to inactivity during warm mid-day hours. The trend of having greater population estimates during winters than autumns, even with different number of observers between years, further suggests that availability bias needs to be investigated.

Nilgai.—Variation in nilgai population estimates among seasons may have been caused by nilgai movements. Average home range size of female and male nilgai in South Texas is 5,500 ha and 7,000 ha, respectively (Moczygemba et al. 2012), and also is highly variable (571–29,909 ha, Foley et al. 2017). The large home ranges indicate great potential for movement; home ranges of nilgai can exceed the ranch scale (e.g., Santa Rosa is 7,471 ha and El Sauz is 11,021 ha). Seasonal movements could occur between surveys, resulting in changes of population sizes. For instance, peak reproductive season in Texas occurs during March and depending on the breeding system (territoriality or harem defense, Leslie 2008), spatial distribution of nilgai may be different during February than November. Commercial hunting during our study on El Sauz may have resulted in emigration but nilgai are not expected to move off-site as a response to hunting (Foley et al. 2017). Thus, differences in our population estimates may be due to large space-use of nilgai.

Feral swine and collared peccary.—Population estimates for both species were inconsistent. Because total number of observations were lowest during the first survey (Nov 2013), inexperienced observers were probably missing these relatively small mammals. We also acknowledge the variability that is potentially present in our estimates by combining data for 2 species. Ideally, future surveys will increase size of study sites or sampling effort to allow for a sufficient number of detections to estimate each species' population size but may be difficult given their relatively larger group sizes. However, our finding of high $g(0)$ (range = 0.82–0.93) shows that distance sampling may be a viable technique to survey feral swine and collared peccary in rangelands. Our conclusion that distance sampling may be useful for feral swine and collared peccary is critical on 2 fronts. First, no population estimation protocol exists in Texas for collared peccary (Taylor and Synatzske 2008). Further research should consider whether distance sampling is a viable technique to estimate population size of collared peccary as it relates to management goals.

Secondly, feral swine are an invasive species that can cause crop damage (Reidy et al. 2008), nest depredation (Dreibelbis et al. 2008), and disease outbreaks (Cooper et al. 2010). Documenting high $g(0)$, albeit estimated with <60 observations, indicates distance sampling is a promising technique to monitor feral swine populations as it relates to management actions (Campbell et al. 2010, Gentle and Pople 2013).

MRDS Versus DeYoung's Correction Factor

White-tailed deer population estimates from MRDS during both autumns were roughly a third lower than those calculated using DeYoung et al.'s (1989) correction factor. The correction factor attempts to correct for both visibility and availability bias while the MRDS technique does not account for availability bias (DeYoung et al. 1989). Given the dense canopy cover associated with Tamaulipan thornscrub region in southern Texas, the discrepancy between MRDS estimates and corrected population estimates is arguably a result of deer unavailable to be detected akin to cetaceans being underwater during surveys (Laake et al. 1997). However, the difference between MRDS and DeYoung's method could also be influenced by protocols used to establish the correction factor. For instance, during the DeYoung et al. (1989) study, helicopters contained 2 observers (vs. our 3 observers), flew at 23 m AGL (vs. 15 m) at 56 kmh (vs. 65–85 kmh), some radio-collars failed during the study that may have affected the mark-resighting calculations, and GPS equipment were not used. Thus, to best evaluate the extent of availability bias, mark-resight studies with current technological advances (i.e., GPS radio-collars) should be conducted.

MANAGEMENT IMPLICATIONS

Mark-recapture distance sampling corrects for imperfect detection on the line and yields less biased population estimates than conventional distance sampling. However, high visibility of large mammals on the survey line during aerial surveys in rangelands reduces the value of MRDS relative to CDS because of the large effort and high additional costs associated with preserving observer independence. A reasonable alternative could be to use CDS or MCDS and then increase population estimates and standard errors by 10% to account for the small proportion of animals missed on the line. But species-specific population estimates were typically lower prior to leaf-fall than post leaf-fall, which suggests that availability bias, or animals that simply cannot be observed, was greater during autumn surveys relative to winter surveys. Additionally, population estimations for white-tailed deer, using a previously published correction factor that accounts for white-tailed deer unavailable to be seen were ~35% greater than our autumn MRDS estimates. Availability bias, which cannot be accounted for with MRDS, needs to be evaluated in future studies of aerial surveys of large mammals in rangelands.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the current article at the publisher's website. Supporting information includes distance bins (SF1), targeted versus actual coverage (ST1), distribution of observations as it relates to habitat type (ST2), MCDS model results (ST3), MRDS statistics for collared peccary and swine (ST4), MRDS density estimates for collared peccary and swine (SF2), density estimates for each of collared peccary and swine (ST5), and breakdown of costs to conduct MCDS (ST6).