DEER DENSITY ESTIMATION IN WEST-CENTRAL TEXAS: OLD VERSUS NEW GROUND TECHNIQUES WITH MARK-RESIGHT AS A COMPARATIVE BASELINE

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Abstract: Population estimation is an important yet often difficult task for wildlife managers. Convenience methods such as spotlighting deer (Cervidae) from roads are often used as trend indices, but with nonrandom survey design, inference is restricted to the area adjacent to roads. The relationship to a greater spatial extent remains unknown. Our primary objective was to examine ‘presumable biases’ in density estimates from road-based nighttime deer surveys in west-central Texas using an area-conversion technique assuming 100% detectability and line-transect distance sampling. We used mark-resight, demographic, and radiotelemetry data to generate a population-level density estimate as an independent comparative standard at the study-site spatial extent. We also compared spotlighting (SL) and thermal infrared imaging (TIR) methods. We hypothesized that deer habituation behavior interacting with roads as semi-permeable barriers to movement would cause clustering near roads at a spatial extent greater than the effective strip width of road survey transects. We predicted that deer density estimates by distance sampling, although descriptive of the area next to roads, would be biased high in comparison to the mark-resight estimate at the spatial extent of the study site. Also, area-conversion density estimates, although biased low due to incomplete detection, may actually provide accurate density estimates at the study-site spatial extent due to deer clustering near roads. We falsified the latter prediction but found support for the former. For inference to the study-site spatial extent, area-conversion estimates consistently appeared biased low, but distance sampling by TIR appeared biased high. Mean group size was greater by TIR than SL affecting density estimates by distance sampling similarly, thus increasing positive bias over SL. Spotlight distance sampling with the hazard-rate model appeared to provide the least biased deer density estimate at the study-site spatial extent. Similar results may be expected in other areas where habituated terrestrial mammals are surveyed from roads. Further study is needed to investigate road effects on deer distributions both within and beyond the effective strip width. This pilot study may be used to design and make predictions for a broad-scale calibration study relating nonrandom survey data to more defensible population estimates.

Key words: area-conversion, density estimation, distance sampling, Odocoileus spp, mark-resight, spotlight, techniques, Texas, thermal infrared, transect
Reliable estimates of animal abundance or density over time are regularly required for effective management but are often expensive and difficult to obtain (Caughley and Sinclair 1994, Lancia et al. 2000, Rabe et al. 2002). There are a variety of methods to estimate animal abundance, and biologists compare techniques to suit their needs (Schwarz and Seber 1999, Borchers et al. 2002, Witmer 2005, Fickel and Hohmann 2006, Msowffe et al. 2007, Viewel et al. 2007). However, many studies do not present a theoretically unbiased estimate of animal abundance or density to which alternative methods of interest can be compared (e.g., Garner et al. 1995, Naugle et al. 1996, Koerth et al. 1997, Smart et al. 2004, Drake et al. 2005, Collier et al. 2007); in such cases, comparisons among methods are only relative and true accuracy or bias cannot be assessed (Gill et al. 1997).

Indices from convenience methods such as spotlight counts of deer (Cervidae) may be useful as trend data, but with nonrandom survey design, inference cannot be extended past the area adjacent to roads (Thompson et al. 1998). Nonrandom survey estimates could be calibrated to more defensible population-level estimates by regression analysis of paired data (Eberhardt and Simmons 1987). These latter data are more rare and difficult to obtain, and unaccounted heterogeneous detectability among surveys may confound results (Lancia et al. 1996, 2000; Pollock et al. 2002; Anderson 2001, 2003). Regardless, spotlighting continues to be a common technique receiving review and refinement without attempts at calibration (McCullough 1982, Fafarman and DeYoung 1986, Cypher 1991, Scott et al. 2005, Collier et al. 2007).

Before 2005, Texas Parks and Wildlife Department (TPWD) used a strip transect area-conversion technique to estimate deer densities assuming 100% detectability at distances out to 229 m from roads (Young et al. 1995). Following Wildlife Management Institute ([WMI]; 2005) recommendations to use probability theory in sampling methods, TPWD changed their white-tailed deer (Odocoileus virginianus) road survey protocol to line-transect distance sampling (Buckland et al. 2001). Our main objective was to examine bias in the former and revised TPWD white-tailed deer nighttime survey techniques at our study site in west-central Texas. Also, we used spotlighting (SL) and thermal infrared imaging (TIR) methods simultaneously for comparative purposes. Because detectability of deer in brush habitats is likely to be <100%, we predicted that the old area-conversion technique would underestimate deer density near roads (Burnham and Anderson 1984). However, at a spatial extent greater than the effective strip width, habituation behavior may result in a clumped distribution of deer near roads if roads are semi-permeable barriers to movement (Haskell et al. 2006), and particularly so if data are collected during environmental conditions that promote deer movement.

Therefore, we predicted that: 1) negative bias of the old area-conversion technique may offset positive bias created by deer habituation behavior, and 2) density estimates based on distance sampling, although more representative of deer densities near roads, would be positively biased for inference to the study-site spatial extent. We present an independent, theoretically unbiased mark-resight population estimate, converted to density using deer location data, as a density estimate at the study-site spatial extent for confirmation of results. Without replication, inference from this study is limited but may be informative and useful as a hypothetico-deductive pilot study (Witmer 2005).

Study Area

We conducted our study on 4 contiguous private ranches (261 km²) in northwest Crockett County, Texas (lat/long: 31.00°N, 101.73°W), during 2004–2006. Topography was varied with southern and eastern portions being mostly flat, while the western and northern portions included mesas (Fig. 1). Elevation ranged from 730–880 m ASL in the southern riparian corridor to mesa tops, respectively. At the nearest National Oceanic and Atmospheric Administration (NOAA) weather station (Big Lake, Texas; ~32 km), the mean daytime high
temperature for November 1971–2000 was 18.7°C, and the mean nighttime low was 4.0°C (NOAA 2005). Mean annual precipitation was 47.5 cm (NOAA 2005).

In the intermittent riparian corridors, herbaceous vegetation was common with some grasses and forbs growing >0.5 m tall under scattered thickets of hackberry (*Celtis reticulata*) and walnut trees (*Juglans microcarpa*). Outside of the riparian corridors, bottomlands had two dominant shrub communities: mesquite (*Prosopis glandulosa*) on relatively mesic soils and a creosote (*Larrea tridentata*)-tarbush (*Flourensia cernua*) mix on well-drained soils. Prickly pear (*Opuntia* spp) and other cactus species occurred in the lowlands, much of which had been heavily grazed by cattle and sheep. Algerita (*Mahonia trifoliolata*), catclaw acacia (*Acacia greggi*), lotebush (*Ziziphus obtusifolia*), and tasajillo (*Opuntia leptocaulis*) were also interspersed primarily throughout the lowlands. The slopes and mesa tops were dominated by juniper (*Juniperus pinchoiti*) communities with sparse varying herbaceous vegetation. Slopes and rimrock areas often contained sotol (*Dasylirion wheeleri*) and yucca (*Yucca* spp).

Land-use was primarily livestock ranching, but low-pressure lease hunting (Butler and Workman 1993, Brown and Cooper 2006) and oil and gas extraction were also common. Secondary roads were dense, and road quality varied from a paved county road to two-track unimproved ranch roads, but maintained caliche roads of intermediate quality were also present (Fig. 1). Both white-tailed and desert mule deer (*O. h. eremicus*) were present at the site in near equal abundance (Brunjes et al. 2006). White-tailed deer tended to select lowland habitats, and mule deer tended to select habitats near mesas, but there was considerable overlap in space use (Avey et al. 2003, Brunjes et al. 2006).

**Methods**

**Field data**

In April 2004 and 2005, we captured 50 adult does (25 mule deer and 25 white-tailed deer) using a net-gun fired from a helicopter (Holt Helicopters, Uvalde, Texas, USA; Krausman et al. 1985). We determined pregnancy by ultrasonography (Smith and Lindzey 1982, Stephenson et al. 1995). We fitted each pregnant doe with a vaginal implant transmitter (VIT; Advanced Telemetry Systems [ATS], Isanti, Minnesota, USA; Carstensen et al. 2003, Bishop et al. 2007), a radiocollar (Telonics, Mesa, Arizona, USA and ATS, Isanti, Minnesota, USA), and a numbered ear-tag. We used the VITs to help locate true neonates for capture, with birthing period peaks near 20 June for white-tailed deer and 20 July for mule deer (Haskell et al. 2007, 2008). When neonates were found, we fitted them with expandable radiocollars (ATS, Isanti, Minnesota, USA; Diefenbach et al. 2003) and numberless ear-tags placed in opposite ears for twins. We used a telescopic vehicle-mounted null-peak antenna system (Balkenbush and Hallett 1988) to radio-track deer year-round. We estimated radiotelemetry locations by weighted-incenter and maximum likelihood methods (Haskell and Ballard 2007). We recorded incidental observations of marked deer with a handheld global positioning system (Model GPS 76; Garmin International Inc., Olathe, Kansas, USA). Radiocollared deer provided estimates of reproductive and survival rates from 2004–2007.

For mark-resight population estimation, we recorded all observations of deer from 22 October 2004–5 February 2005 as the first “closed” primary sampling period (i.e., year) and again from 8 October 2005–29 January 2006 as the second “closed” primary sampling period. We opportunistically recorded deer by age class (i.e., fawn or adult), gender, and species while traveling roads. We were careful not to allow our knowledge of an animal’s location while radio-tracking affect our visual search patterns by standardizing search patterns. Radio-tracking deer was usually performed >1 km away from the animal (Haskell and Ballard 2007), but roads would at times lead us closer which should not in itself violate the assumption of equal sightability of marked and unmarked deer where surveyed. We did not record observations when backtracking dead-end roads to achieve independent observations within secondary sampling.
We only made observations from roads within the home-ranges of our marked deer (Fig. 1). When a radiocollared deer was observed, we used binoculars to read the ear-tag on adults and verify ear-tag location on fawns and a VHF radio-receiver with the null-peak dual-yagi antenna to identify which individual was spotted.

We conducted night surveys from 4–6 November 2005 consistent with TPWD protocols except that TPWD surveys were typically conducted from August–October (Shult and Armstrong 1999, Young et al. 2005); we surveyed later in the season to be closer to the breeding period when deer should be more active (S. Haskell, unpublished data). We limited surveys to environmental conditions that may promote deer movement and feeding behavior (e.g., low winds and no precipitation). We began surveys about 1 hr after sunset (1900 hrs) and stopped by midnight. We used spotlighting (SL) and thermal imagery (TIR) simultaneously to compare number of deer observed and overall density estimated by each method. Because it was easier to survey a greater area by SL than TIR at a given speed, we only observed one side of a road.

Figure 1. Study site for 2004–2005 deer surveys in northwest Crocket County, Texas, showing topography, individual deer locations, and minimum convex polygon (MCP) of all locations with 884-m buffer as effective sample area estimates. Main secondary caliche road surveyed leaves paved road near northeast corner, heads west, and splits through two mesa valleys headed northwest and southwest. All secondary ranch roads including some across mesas not available for plotting from available databases (e.g., ESRI and USDOT Bureau of Transportation Statistics).
during a survey. We selected 5 roads that ranged across the study site within the home-ranges of our marked deer. We selected the most used and best maintained roads including the north-south paved road and the 2 main east-west caliche roads (Fig. 1). Effective strip width of all selected roads included all vegetation community types. We surveyed the 3 main roads in both directions and the other 2 one-way only. Because the same roads were surveyed on different nights and opposite sides contained differing proportions of habitat types, we considered each pass as a separate transect. During 1 evening temperatures dropped to near freezing, and we observed deer bedded more than during previous surveys, so we stopped the survey short about halfway through a transect and considered this survey to be a unique transect. Thus, we surveyed 9 transects with mean length of 5.83 km (range = 3.19–7.58 km). We used a Suunto® Navigator sighting compass (Suunto, Vantaa, Finland), a Bushnell® Yardage Pro Scout laser range-finder (Bushnell Performance Optics, Bausch & Lomb, Inc., Overland Park, Kansas, USA), a portable thermal infrared imaging camera (PalmIR® 250 Digital, Raytheon Commercial Infrared, Dallas, Texas, USA), and a 100,000 candle power spotlight (SHO-ME® model #:08.0375.012, Wistol Supply, Dallas, Texas, USA) to locate deer groups and find the direction and distance (m) to the center of groups. The spotlight used was lightweight with sharp beam focus effective for shining eyes at long distances and was keeping with TPWD protocols. Most groups were identifiable by species but several were not. To maximize precision of density estimates we did not stratify data by species, and we could not hypothesize any a priori cause to do so for our current objectives.

Our crew consisted of 4 people: a driver, a TIR observer, a SL observer, and an additional data recorder. We drove at 11–13 kph (7–8 mph). The driver helped spot deer on and adjacent to the road to help ensure 100% detectability on the transect line and recorded location data by GPS when observations were made. We mounted the thermal imaging camera onto an adjustable tripod and placed it on the cab of the truck (~3 m AGL). We routed the display to a portable DVD player (Model: IS-PD101351, Insignia, Richfield, Minnesota, USA) with a 22.9 cm screen. The TIR observer stood at the front of the truck bed and searched for deer by watching the TIR monitor. The additional data recorder estimated distances to deer and recorded TIR data only. The SL observer was positioned at the rear of the truck bed and did not watch the TIR monitor. When deer were observed, the observers found reference points (e.g., shrub, large stone, sign, fence post, etc.) at the animal’s initial location because the truck was not immediately stopped to allow the other observer a chance to find the group of deer; we measured distances to reference points. Texas Parks and Wildlife Department procedures call for 80% of observation effort to be in the front half of the viewing area (i.e., 0–90° in relation to the vehicle’s heading) and only 5% in the last quarter (135–180° to the vehicle’s heading), so the truck was stopped when a group of deer had entered the last quarter of the viewing area to maximize independence of observations between observers. At that time the reference point’s azimuth and distance were recorded as was the deer count by each observer successfully locating the group. For comparative purposes, we considered observations between nighttime methods suitably independent with identically distributed deer.

Mark-resight density estimation

We used the robust design beta-binomial closed population mark-resight model to estimate deer abundance at our study site (McClintock et al. 2006). We used model averaging results with log-normal confidence intervals (McClintock et al. 2006). This model allowed for heterogeneity in sighting probabilities among individuals, as we opportunistically surveyed some roads more frequently than others. The robust design model used data from both primary sampling periods (i.e., years) to estimate sighting probability parameters, thus maximizing precision. Demographic closure within primary sampling periods was violated due to the length of time necessary to obtain adequate sample sizes. To account for deer mortality within primary sampling periods, we used known-fate data from radiocollared deer and estimated the total
number of marked deer as the sum of individual proportions of survey availability. We calculated individual survey availability as the number of secondary sampling occasions (i.e., days) an individual was alive divided by total number of secondary sampling occasions. The assumption of geographic closure was also violated. Methods to account for potential bias in density estimation using telemetry data to adjust the abundance estimate were not possible for our opportunistic surveys (White and Shenk 2001), so we used radiotelemetry data to estimate a range of effective area sampled (Soisalo and Cavalcanti 2006). Omitting two brief prepartum (i.e., springtime) extralimital forays, we drew a minimum convex polygon (MCP) around radiotelemetry locations of all 50 adult marked deer captured in 2004 and available for sampling in 2005. Because the roads used for mark-resight observations were widespread within this area with some exception at the western edge (Fig. 1), we considered this a minimum estimate of the effective area sampled. Next we calculated MCP home-range areas for each marked individual excluding point location outliers by groups of 1, 2, or 3 that accounted for at least 15%, 30%, and 45%, respectively, of total home-range size for an individual. Assuming a circular home-range shape, we calculated a home-range radius for each individual and used the overall mean to draw a buffer around the original MCP (Fig. 1). The area within the outer edge of the MCP buffer was our maximum estimate of effective area sampled.

We estimated the 2004 population size based on the doe mark-resight estimate. Because surviving marked fawns were few, resighting probabilities were low, and fawn:doe mark-resight ratios were much lower than predicted by known-fate data, we estimated the fawn population according to reproductive rates (1.9 fetuses/doe) and cumulative survival (57%) by Cox regression through the mid-survey period (S. Haskell, unpublished data). We estimated the adult buck population according to the 1:2.5 observed buck:doe ratio. In all cases where a portion of the population was estimated from the mark-resight doe estimate, we extrapolated 95% confidence intervals and point estimates, so confidence intervals grew with each estimated parameter. To predict and refine the subsequent 2005 mark-resight population estimate, we projected the 2004 estimate 1 year forward using vital rate data from radiocollared adult does and fawns. We estimated doe survival at 95% which was conservative given that only 1 of 50 does died between birthing periods of 2004 and 2005. We estimated buck survival at 90% given minimal hunting pressure (~1 buck taken/6 km²). We estimated fawn recruitment from 2004–2005 similarly as before from the 2004 mark-resight doe estimate with annual fawn survival (55%) and doe productivity data. We estimated the surviving 2005 fawn population present during the mid-survey period as the additive product from adult does surviving from 2004 and the product from yearling females. We assigned lower productivity (1.1 fawns/doe) and fawn survivorship (37%) to yearling does than for adult does (1.9 fawns/doe, 47% fawn survivorship; S. Haskell, unpublished data).

Because the separate mark-resight fawn:doe ratios were in concordance with known-fate data in 2005 (S. Haskell, unpublished data), we used the combined doe-fawn mark-resight estimate to maximize precision of the base estimate for 2005. To this we added the buck portion of the population based on the 1:2.5 buck:doe ratio observed again in 2005.

Night survey density estimation

We used prior TPWD protocol for the area-conversion density estimator (Young et al. 1995). Any deer group observed beyond 229 m (250 yd) was discarded from the analysis. Every 161 m (0.1 mi) along a transect, we used the laser-rangefinder to estimate the distance perpendicular to the road that a deer could be seen by spotlight through brush; this estimate was subjective but has been shown to be similar among observers (Whipple et al. 1994). If topography caused 0% detectability at some mid-range of distance, then distance was taken to the near-side of the obstruction and no deer groups were recorded beyond. Perpendicular distance estimates were averaged within transects; this mean was considered the effective strip width and multiplied by the length of the transect to estimate the effective area surveyed; the
number of deer observed was divided by the area estimate to obtain the density estimate for the transect. Means and measures of variability were calculated among transects as the final descriptive statistics for deer density by area-conversion. We present statistics for SL and TIR independently and in combination where the greater number of deer observed between the 2 methods was assigned to each group.

For line-transect distance sampling analyses of clustered data, we used combinations of the 3 key functions with 2 series expansions recommended by Buckland et al. (2001:47) and selected models within and among key functions by lowest Akaike’s information criterion (AIC). Based on a larger region-wide dataset collected by TPWD in 2005 and 2006 (M. Lockwood, TPWD, personal communication) and the results of Gill et al. (1997), we did not use a group size adjustment for estimating the detection function. Similar to the area-conversion technique, we right-truncated data at the farthest observation <229 m. Sampling fraction was 1/2 because we only surveyed one side of a transect. We present chi-square goodness-of-fit statistics based on default software results considering the data distribution with greatest number of distance bins while allowing some pooling at farthest distances. Also, this data distribution was preferred to illustrate a peculiarity identified in our data during preliminary inspection. Given the many assumptions underlying our data, violated and remediated to varying degrees, we made qualitative comparisons among methods by examining expectations of means and 95% confidence intervals (Cherry 1998).

We used MapSource™ 4.09 (Garmin Inc.) to measure transect lengths and generate stopping points to estimate sightable distances for the old TPWD method; SAS® 9.1 (SAS Institute Inc., Cary, North Carolina, USA) to execute the mark-resight estimator; MATLAB® 6.5 (The MathWorks, Natick, Massachusetts, USA) to estimate radiotelemetry locations, locate MCP hull points, and calculate individual MCP home range areas; ArcGIS™ 9.1 (ESRI, Redlands, California, USA) for mapping and generating an MCP buffer; Distance© 5.0 Beta 5 (Thomas et al. 2005) for distance sampling analyses; and S-Plus® 7.0 (Insightful Corp., Seattle, Washington, USA) for data plots.

Results

Mark-resight density estimation

In 2004, we had 31 secondary sampling occasions and included does with live radiocollars from a previous study that were known to live in the core study area. We began the primary sampling period with 59 marked does and 22 marked fawns in the survey area. Zero does and 1 fawn died during the sampling period, and 1 fawn emigrated for 13 of 31 secondary sampling occasions. Thus, we estimated 59 marked does and 21 marked fawns available during the primary sampling period. We recorded 433 observations of deer of which 167 and 15 were unmarked and marked does, respectively, and 134 and 4 were unmarked and marked fawns, respectively. We were unable to classify 30 unmarked adults by gender, so we assigned them to gender according to the observed 1:2.5 buck:doe ratio which included more observation data from outside the survey area. Individual resighting frequencies of the 59 marked does were low and were 46, 11, and 2 for 0, 1, and 2 resight occasions, respectively. The doe population was estimated to be 779 individuals (95% CI = 531–1157, CV = 0.201), and variability around the total population estimate was even larger (Fig. 2). The population estimate projected from these data into 2005 was 2661 individuals (95% CI = 1793–3953, Fig. 2); we considered this estimate conservatively low given demographic vital rates used.

In 2005, we had 28 secondary sampling occasions and also included surviving marked female fawns from the previous year in our adult marked sample. We began the primary sampling period with 58 marked does and 27 marked fawns. Three does and 6 fawns died and 1 fawn dropped a collar during the sampling period resulting in an estimated 56 and 25 marked does and fawns, respectively, available during the primary sampling period. Two does were
shot in a single incident after the 18th secondary sampling period; these does were 2 of our most sightable individuals, so the mark-resight estimate may have been slightly biased high. We recorded 704 observations of deer of which 298 and 14 were unmarked and marked does, respectively, and 232 and 6 were unmarked and marked fawns, respectively. We were unable to classify 32 unmarked adults by gender, and we assigned them to gender as above. Individual resighting frequencies of the 56 marked does were low and were 44, 10, and 2 for 0, 1, and 2 resight occasions, respectively. The combined doe-fawn population estimated by mark-resight was 2440 individuals (95% CI = 1731–3453, CV = 0.178). To this we added the buck portion based on the doe-only mark-resight estimate of 1382 individuals (95% CI = 932–2064, CV = 0.205) to yield a total population estimate of 2993 individuals (95% CI = 2104–4279, Fig. 2).

We used 3478 point location estimates, with mean estimated linear error by beacon study equal to 94.4 m, to calculate the MCP study-site home-range of the 50 deer captured and marked in 2004 (mean = 70 locations/deer, range = 40–117; Fig. 1). The area within the MCP was 85.3 km² which was our minimum estimate of effective area sampled. From the original 3478 point locations we identified 55 outliers within individual home-range plots. These outliers represented 1.6% of the total number of points but accounted for 37.8% of total individual home-range areas. After removing the outliers, mean individual home-range radius was 884.3 m (SE = 30.1, range = 511–1525). The area of the outer MCP including this buffer was 119.5 km² which was our maximum estimate of effective area sampled (Fig. 1). Considering both the projected and mark-resight population estimates in 2005, we considered a population range of 2600–3050 deer in 2005 to be reliable given predicted potential biases in dual estimates for 2005 (Fig. 2). By dividing the lower population estimate by the higher effective sample area estimate, and conversely, the higher population estimate by the lower effective sample area estimate, we obtained a robust estimate of deer density at our study site of 21.8–35.7 deer/km² (Fig. 3).

**Figure 2.** Mark-resight population estimates from winter deer surveys in northwest Crockett County, Texas, 2004 and 2005. Estimate from 2004 projected into 2005 based on unpublished demographic vital rate data for a priori prediction and post hoc refinement of 2005 estimate. Larger ellipse illustrates combined 95% confidence intervals, and smaller ellipse illustrates subjective determination of a reliable estimated range of 2600–3050 deer in 2005.
Figure 3. Deer density estimates by nighttime surveys in northwest Crockett County, Texas, during November 2005 with a mark-resight (M-R) estimate as an independent comparative baseline. Estimates are from area-conversion (assuming 100% detectability) and distance sampling techniques using spotlighting (SL), thermal infrared imaging (TIR), and combined (C) methods. Error bars are 95% CIs around expected means.

Night survey density estimation

We observed 86, 86, and 101 deer groups by SL, TIR, and combined SL-TIR, respectively. Each method failed to detect 15 groups detected by the other. We detected 179, 198, and 219 individuals resulting in mean group (i.e., cluster) sizes of 2.08 (SE = 0.21), 2.30 (SE = 0.24), and 2.17 (SE = 0.21) by SL, TIR, and combined SL-TIR, respectively. Effective strip width estimates among the methods were similar (Table 1). Thus, the main difference between SL and TIR was the ability of TIR to detect more individuals within groups on average. Of the 21 individuals detected by SL and missed by TIR, 0, 3, and 8 were within the first 3 SL goodness-of-fit distance intervals (i.e., <52.2 m), respectively (Fig. 4). Of the 40 individuals detected by TIR and missed by SL, 0, 3, and 11 were in similar TIR distance intervals <48.0 m (Fig. 4). These results suggested that detection probability within about 20 m of the line was excellent for both methods but did decrease consistently out to 50 m contrary to the preferred hazard-rate model expectations with relatively wide shoulders of g(x) = 1 (Fig. 4). Therefore, the hazard-rate model may be biased low when describing the density of deer next to roads (Table 1). There appeared to be a micro-scale redistribution of deer relative to roads with some avoidance out to about 30 m and clumping from 35–55 m (Fig. 4).

Among transects, the mean sightability distance estimated for the area-conversion technique was 122.4 m (SE = 8.5 m, range = 81.4–155.5 m). Estimated mean density varied among methods (Fig. 3), but using the more popular SL method as an example, density estimates among transects varied widely (mean = 20.8 deer/km², SE = 4.3, range = 6.1–42.6 deer/km²). Our area-conversion density estimate by SL was significantly less than that by mark-resight (Fig. 3). Locating more deer, the TIR point estimate was greater than SL, but only when the two methods were combined to maximize the number of deer observed did an estimate approach that of mark-resight (Fig. 3); such an approach would be logistically prohibitive in large-scale application. Precision for both the area-conversion and distance sampling techniques was poor due to few transects with relatively large variability among transects (Table 1).
Due to influences of human use (e.g., livestock water tanks and feed) and other habitat heterogeneity, substantial variability among transects was probably legitimate. For all methods, the distance sampling hazard-rate key function was the best fit model, required no series expansion, and seemed to split the lack-of-fit area <60 m from the road transect well (Table 1, Fig. 4). Fit was poor in all models due mostly to the peak at 35–55 m. The difference in expected density between the SL and TIR hazard-rate models was due primarily to the difference in mean group size, whereas the difference in expected density between TIR and combined methods was due primarily to estimated density of clusters with the additional 15 deer groups (Table 1). Overall, the hazard-rate distance sampling model by SL technique appeared to provide the least biased point estimate of density at the study-site spatial extent using the mark-resight data for confirmation (Table 1, Fig. 3).

Table 1. Results from nighttime distance sampling of deer from roads in west-central Texas, November 2005, including method used (SL = spotlight, TIR = thermal infrared imagery), model (HN = half-normal, HR = hazard-rate, U = uniform), series expansion (CO = cosine with no. orders of adjustment in parentheses, NA = not any), no. estimated parameters (K), goodness-of-fit p-value, AIC difference, and expectations of deer density (no. per km²), effective strip width (ESW; m), and cluster density (no. deer groups/(no. km surveyed×ESW×0.1)). Coefficients of variation (CV; SE/mean) given after ESW and density estimates. Different observations preclude AIC comparisons among methods.

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Discussion

There is a need for simulation and field studies assessing methods to estimate effective area sampled in geographically open populations sampled without trapping grids. Given the relatively small home ranges and spatial concentration of marked deer at our study site and predefined survey boundaries within a comprehensive road system, we feel that our estimated range of effective area was justified (Fig. 1). This coupled with our dual approach to estimating population size in 2005 (Fig. 2) should have produced a robust estimated range of true overall deer density. Furthermore, our general predictions of potential bias in the former TPWD area-conversion and revised TPWD distance sampling techniques appeared validated. Due to disproportionate observation effort near the center of our study site and generous estimates of
individual home-range areas, we suspect that the outer MCP buffer may have overestimated effective area sampled. Thus, the true central tendency of the mark-resight density range may have been at least 30 deer/km² rather than 29 deer/km² and very near the distance sampling point estimate of 31 deer/km² by SL (Fig. 3). Without replication in time and space, we restrict inference from our results to northwest Crockett County, Texas, on the nights we conducted our surveys. However, apparent technique biases were as predicted a priori, and we expect that they will hold true for future analyses of deer density estimation from nighttime road surveys. Distance sampling from line transects assumes 100% detectability on the survey line, accurate distance and angle measurements, animals are not counted twice during a survey, detection of animals at initial locations, and randomly located transects (Buckland et al. 2001). Our methods should have satisfied the first 3 listed assumptions with little question. However, the data indicated fewer deer observed <35 m than would be expected with a tall peak from 35–55 m (Fig. 4), thus raising concerns for the last 2 assumptions. Others observed fewer deer than expected on and directly adjacent to roads (Kie and Boroski 1995, Ward et al. 2004), and it appears to be a statewide phenomenon in Texas (M. Lockwood, TPWD, personal communication). Previous observations were that deer were not moving away from the transect line before initial detection during surveys (Kie and Boroski 1995, Ward et al. 2004). Based on our careful attention to initial locations and deer movement behavior, we concur. We believe that these data distributions (Fig. 4) were the result of micro-scale avoidance of roads by deer before potential disturbance by observers. This relates to the last and most violated assumption of distance sampling from roads – randomness.

Roads do not offer a random sample of the landscape and can affect results in several ways (Rost and Bailey 1979, Varman and Sukumar 1995, Yost and Wright 2001, Ruette et al. 2003, Haskell et al. 2006). Wildlife managers such as those in Texas often rely on road surveys to cost-effectively sample large areas, although arguments have been made for less data that are more reliable (Rabe et al. 2002, WMI 2005). The wide detectability shoulder of the hazard-rate model characteristically produced the lowest (Buckland 1985) and apparently least biased density estimates (at the study-site spatial extent) compared to the uniform and half-normal models despite the fact that neither the SL or TIR method exhibited 100% detection from 18–50 m (Table 1, Figs. 3 & 4). The hazard-rate model may provide a more efficient estimate of the expected probability density function at distance = 0 than other models when relatively few animals are seen directly adjacent to the centerline (Buckland 1985). A pre-survey micro-scale avoidance behavior affecting results may be synonymous to movement in response to the observer but may be less correctable. Left truncation seems unjustified because distributional consequences of such a behavioral effect may inversely influence densities at farther distances as suggested by our peaked data (Fig. 4; Buckland et al. 2001). Turnock and Quinn (1991) explored a decomposition approach for movement towards the centerline which is a plausible scenario for deer habitat selection in certain circumstances, and Buckland and Turnock (1992) developed a dual platform method to record auxiliary data for movement away from the line which was refined by Palka and Hammond (2001); none can be applied to our case study. We used a monotonically decreasing detection function to reduce the bias introduced by animals avoiding the survey line (Laake 1978, Turnock and Quinn 1991). However, a standard solution to this problem seems unavailable without grouping data, thereby sacrificing accuracy and precision (Southwell and Weaver 1993, Buckland et al. 2001), but this may be acceptable for large datasets. Further investigation into this problem seems warranted (Cassey and McArdle 1999).
Figure 4. Detection probabilities versus distance from roads resulting from preferred hazard-rate distance sampling models of nighttime deer survey data from northwest Crockett County, Texas, in November 2005 by spotlighting (SL), thermal infrared imaging (TIR), and combined methods. Histogram bins scaled according to goodness-of-fit test as observed frequency divided by expected. Interval cut-points are multiplicative of 17.4 m for SL, 16.0 m for TIR, and 15.1 m for combined as default output data from the program Distance.
Criticisms of nonrandom road surveys usually cite habitats and human use as two principle potential confounding factors (Buckland et al. 2001). Similar to Gill et al. (1997), we felt that our road transects included representative habitats of our study site. Also, hunting was minimal and distributed as much away from our roads as it was near so should not have induced large-scale avoidance. These concerns should be considerations for all nonrandom surveys in design and analyses. Instead, we had an a priori reason to consider a large-scale (i.e., beyond the survey strip width) clumping effect near roads as the result of habituation behavior in deer interacting with roads as semi-permeable barriers to movements (Haskell et al. 2006). The micro-scale avoidance effect (Fig. 4) and overall positively biased density estimates by distance sampling from these relatively high-use roads supported this hypothesis (Table 1, Fig. 3); deer densities may have been lesser near less traveled ranch roads. Also, with known reduced detectability after 20 m by both SL and TIR methods, the wide-shouldered hazard-rate model may have been the least biased distance sampling density estimator at the study-site spatial extent because it was negatively biased for predicting observed densities of deer next to roads. Standardizing surveys during environmental conditions that are likely to promote deer movement could allow comparability of results among surveys in this regard, but replication and calibration to more reliable estimators is necessary to help identify and control other confounding factors such as season and habitats (Progulske and Duerre 1964, Eberhardt and Simmons 1987, Whipple et al. 1994, Buckland et al. 2001, Butler et al. 2005).

Biologists have explored the use of TIR to monitor game populations for at least 40 years (Croon et al. 1968, Graves et al. 1972, Wyatt et al. 1980). Technological advancements have included improved resolution and portability of imaging systems, so biologists continue to explore the utility of these systems (Wiggers and Beckerman 1993, Gill et al. 1997, Havens and Sharp 1998, Haroldson et al. 2003, Bernatas and Nelson 2004). Efficacy of TIR may be site-specific (Ditchkoff et al. 2005, Butler et al. 2006). Regardless, comparative evaluations found greater detectability of TIR over SL in nighttime ground-based surveys (Belant and Seamans 2000, Focardi et al. 2001, Collier et al. 2007). Our results also demonstrated that TIR on average detected more deer in groups than SL for which eye-shine is the key to detectability. With greater mean group size for TIR, density estimates by distance sampling were also greater than those by SL. However, if deer cluster near roads relative to a larger spatial extent as appeared evident in our study, the detectability advantage of TIR may increase positive bias in density estimates inferred to the larger extent and thus would be undesirable (Fig. 3).

Research and Management Implications

Nonrandomness in animal surveys is often an undesirable property introducing unexplained variability and limiting scope of inference. However, if care is taken to standardize and calibrate nonrandom survey data to reliable estimates, desirable results may be achieved; this study provides an optimistic beginning. Successful integration of such survey methods will require biologists to recognize, document, and remediate potential confounding factors during design, data collection, and analyses. Spotlight survey data are often used to allot harvest permits on private lands in Texas. Texas landowners often perform their own spotlight surveys using the old area-conversion technique, while TPWD biologists survey the same regions from public roads using the new distance sampling protocols. While our results suggest that landowner estimates should be multiplied by about 1.4, a broader study examining potential methodological, biological, and anthropogenic influences is needed. If spotlight data are collected from paved roads with environmental conditions promoting deer movements, the hazard-rate distance sampling model may be accurate to estimate local deer densities in west-central Texas. These predictions may be true in other areas where habituated wildlife are surveyed from roads. However, more study is warranted to determine effects of roads on deer distributions within and beyond the effective strip width. Results from this pilot study (n=1) may
be used to design and make predictions for a broad-scale calibration study pairing density estimates from roads with estimates from more defensible techniques (e.g., Potvin et al. 2002, 2004; Potvin and Breton 2005).

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Literature Cited


