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Error in demographic ratios from aerial surveys of white-tailed deer in semi-arid rangelands

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Abstract

Aerial surveys can efficiently monitor populations of large animals in geographically extensive management units but are time- and cost-intensive. Biologists often design population surveys to balance cost, spatial coverage, and precision in estimates of population size. Demographic ratio data from aerial surveys are an important component of population monitoring and management, yet the error of ratio data remains under-appreciated, especially for low-density populations. We quantified error in juvenile:female, male:female, and young:mature male ratios from 177 helicopter surveys of white-tailed deer (*Odocoileus virginianus*) in 37 wildlife management units encompassing 3,269 km^2 of semi-arid grasslands and brush in South Texas, USA, during 2011–2015. We classified error (the % difference between the mean and the limits of the confidence interval) of surveys as appropriate for research-based (≤25% error) or monitoring surveys (≤50% error). Overall, error usually met criteria for monitoring surveys but not for research-based surveys; male:female ($\bar{x} = 32\%$ error) and juvenile:female ($\bar{x} = 37\%$) ratios had smaller errors than young:mature male ratios ($\bar{x} = 51\%$). As number of detections increased, errors declined; minimum number of detections for both components of a given ratio needed for monitoring and research-based surveys was about 30–40 and 150–185 at the 90% confidence interval and 45–60 and 210–230 at the 95% confidence interval, respectively. Acceptable error to reliably detect changes in demographic ratios may require greater survey effort or a different survey design for low-density populations. Furthermore, obtaining sufficient detections for acceptable error of male age structure estimates may not be feasible. Error of demographic ratios is an important consideration given their role in the design of harvest plans, evaluation of the effects of management, and tracking the effect of diseases, such as chronic wasting disease. The high effort required to obtain acceptable error with ratio data in areas with low deer densities indicates that helicopter surveys may not be an ideal platform to investigate fine-scale variation in demographic data. Managers will have to consider trade-offs between expenses and variance of ratio data collected from aerial surveys and whether obtaining acceptable error with ratio data is feasible given deer densities and detection probabilities are site-specific.

KEYWORDS

age structure, demographic ratio, error, helicopter surveys, juvenile:female ratio, male:female ratio, *Odocoileus virginianus*, ratio data, sex ratio, white-tailed deer

Aerial platforms are an efficient way to survey wildlife populations over spatially extensive areas (Samuel and Pollock 1981, Bleich et al. 1994, Peterson et al. 2020). Data collected during aerial surveys are used to generate estimates of abundance or population size, adult sex ratios, male age structure, and offspring recruitment rates; all of these are used to direct management or conservation decisions (Gasaway et al. 1986, Zabransky et al. 2016). Sex and age composition and recruitment, commonly expressed as ratios, are often used to assess population status relative to management objectives. For instance, too few males relative to females may require changes in harvest strategies (Ginsberg and Milner-Gulland 1994). Aerial surveys may record age structure of males to quantify effects of management strategies, such as antler point restrictions, intended to encourage survivorship from young to mature ages (Bender and Miller 1999, Biederbeck et al. 2001, Hansen et al. 2017) or control disease (Mysterud et al. 2020, Conner et al. 2021). For example, chronic wasting disease, a fatal transmissible spongiform encephalopathy, affects age and sex composition of populations; prevalence is higher in males and generally increases in older males (Grear et al. 2006, DeVivo et al. 2017). Finally, juvenile:female ratios allow inferences about population growth, density dependence, and habitat quality (Gaillard et al. 1998, Bowyer et al. 2014).

Population estimates derived from aerial surveys incorporate uncertainty because not all animals are seen (Caughley 1977), signified by measures of variation (Pollock et al. 2006, Barker 2008). Precision of population estimates influences the ability to detect changes in population sizes (Cochran 1977); however, ratio data are rarely presented with measures of variation (Ricklefs 1997, Foley et al. 2016, Larter et al. 2017, Frenette et al. 2020). Because of the high costs for flight time, populations are often surveyed once a year; surveys are rarely replicated within a given year (Shupe and Beasom 1987). Therefore, the variation of ratio data must be estimated from a single survey. Oftentimes, variation of a ratio is only considered well after the survey, such as for population modeling (Monteith et al. 2015). When the variation of ratio data is unknown, it can be difficult to determine the effect of harvest management strategies on population parameters (Sæther et al. 2003, Bender 2006).

White-tailed deer (*O. virginianus*) are the most common and widespread species of large mammal in North America (Heffelfinger 2011). In the United States, white-tailed deer are the primary driver of revenue for many state wildlife management agencies via sales of hunting licenses, and taxes on firearms and ammunition

(Hansen 2011). White-tailed deer are managed as a publicly owned, renewable natural resource over a range of management intensities and harvest regimes (Adams and Hamilton 2011). Landowners and state agencies routinely use aerial surveys for the management of white-tailed deer populations (Beringer et al. 1998, Potvin et al. 2004), particularly on rangelands in the southwestern United States (DeYoung et al. 1989, Peterson et al. 2020).

White-tailed deer in semiarid rangelands are not migratory and occur in small groups (~3–5 deer/group; DeYoung and Miller 2011). Helicopter-based detection probabilities of white-tailed deer in southern rangelands are ≤0.50 (DeYoung 1985, DeYoung et al. 1989, Peterson et al. 2020). These are lower than detection probabilities of other species of ungulates, such as elk (*Cervus canadensis*) and mule deer (*O. hemionus*), that are often surveyed where they aggregate on winter ranges (Samuel et al. 1987, Freddy et al. 2004, Phillips et al. 2019). The combination of lower detection probabilities and smaller group sizes could influence the amount of survey effort needed to obtain sufficient detections for ratio data. The number of detections is important because as sample size (detections) increase, variation declines. The point when variation becomes acceptable is somewhat subjective and represents a trade-off between cost, logistics, and need for management. For instance, errors of ±15% (the difference between the mean and the limits of the confidence interval) could be considered appropriate for research-based surveys, whereas errors of ±20–25% could be considered sufficient for intensive population management (Eberhardt 1978, Terrestrial Ecosystems Task Force Resources Inventory Committee [TETFRIC] 2002). Errors of ±50% would be appropriate for less-intensive management or a general monitoring survey without any specific research objectives (Eberhardt 1978, TETFRIC 2002). The recent emergence of chronic wasting disease in white-tailed deer and mule deer in Texas, USA (Texas Parks and Wildlife Department 2022) has brought increased attention to population monitoring (Figure 1). The disease is fatal and poses serious long-term implications for management (Williams et al. 2002, Uehlinger et al. 2016, DeVivo et al. 2017), especially for populations in semi-arid regions, where population growth rate is low because of variable precipitation (Foley et al. 2016, DeYoung et al. 2019, Islam et al. 2022).

To gain a better understanding of error in ratio data from white-tailed deer in semi-arid rangelands, we used 5 years of data collected during helicopter surveys from 37 wildlife management units (WMUs) on 3,269 km^2 of southwestern rangelands. Our objectives were to evaluate error of juvenile:female, male:female, and young:mature male ratios; evaluate factors influencing error of these 3 ratios; and estimate number of detections appropriate for monitoring surveys (≤50% error) and research-based surveys (≤25% error). We predicted that low detection probabilities, small group sizes, and relatively low densities (DeYoung 2011) of white-tailed deer in southwestern rangelands would generate error appropriate for monitoring surveys but not for research-based surveys.

STUDY AREA

Our study took place on the privately owned King Ranch, which encompasses 3,340 km^2 in Kleberg, Jim Wells, Brooks, Kenedy and Willacy counties in South Texas, during 2011–2015. The ranch is divided into 4 non-contiguous divisions: Encino (424 km^2), Laureles (1,043 km^2), Norias (974 km^2), and Santa Gertrudis (826 km^2). Ranch activities balance livestock production with wildlife management, and the ranch derives additional income from leasing trespass rights for hunting. Each division is further partitioned into 4 to 13 WMUs ($n = 37$); each WMU is composed of 1–8 livestock pastures, which are surrounded by 1.2-m net-wire fences. Most WMUs had cattle present; stocking rates were dependent on habitat and environmental conditions. Average WMU size is 81.2 km^2 (range = 27.5–194.0). Harvest is relatively conservative and focused on adult males (Foley et al. 2022), resulting in a robust male age structure. Harvest of females is low because of the influence of variable annual precipitation on recruitment rates (Foley et al. 2016, DeYoung et al. 2019).

The King Ranch lies in the Western Gulf Coastal Plain and Southern Texas Plains Level III Ecoregions (Griffith et al. 2004). Native fauna included white-tailed deer, collared peccary (*Pecari tajacu*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), wild turkey (*Meleagris gallopavo*), and bobwhite quail (*Colinus virginianus*) along with exotic

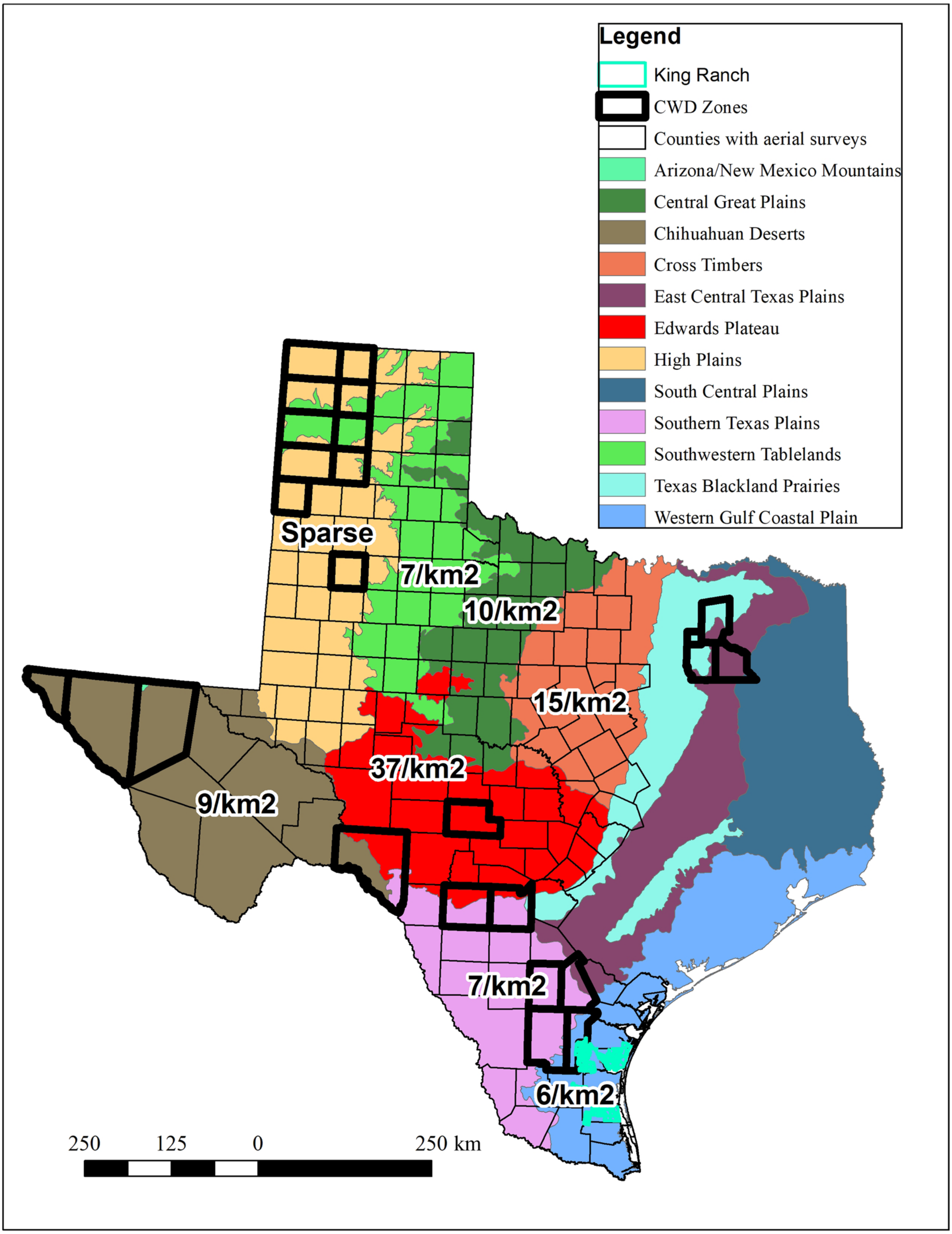

FIGURE 1 White-tailed deer densities at the eco-region level in Texas, USA. Thin black polygons indicate counties containing properties that typically use aerial platforms to conduct surveys for white-tailed deer. Thick polygons indicate counties within chronic wasting disease (CWD) containment zones (Texas Parks and Wildlife Department 2022).

feral pig (*Sus scrofa*) and nilgai antelope (*Boselaphus tragocamelus*). Dominant vegetation communities vary because the transition from coastal sand to interior loamy sand results in a change from coastal grasslands to inland brush communities. The Laureles, Santa Gertrudis, and Encino divisions are primarily Tamaulipan thornscrub, whereas Norias is more diverse, with coastal grasslands and sand dunes on the coast that transition into live oak (*Quercus virginiana*) mottes in the center portion. West of the live oak mottes, the habitat transitions into mesquite (*Prosopis glandulosa*) and huisache (*Vachellia farnesiana*) savannas. Parent et al. (2016) provided additional details. The herbaceous community contains native grasses and forbs interspersed with grasses introduced for their grazing value. Average temperatures are 22.3°C (National Oceanic and Atmospheric Administration [NOAA] 2021) with high temperatures typically observed during August (36.4°C) and low temperatures (18.9°C) during January. Annual rainfall averages 65 cm (NOAA 2021) but is highly variable (CV > 20%; Norwinen and John 2007) with peaks during May and September (Fulbright and Ortega-S 2006).

METHODS

Data collection

During 2011–2015, King Ranch personnel conducted surveys each September prior to the onset of hunting season in October. During this time of the year, juveniles (i.e., fawns) are approximately 3 months old and most adult (≥1.5 years old) males have hardened antlers. Personnel conducted surveys using a 4-seat helicopter (R44, Robinson Helicopter Company, Torrance, CA, USA) with 3 experienced observers in addition to the pilot. The survey protocol was to fly parallel, fixed-width transects (Figure 2) in the helicopter at 56–64 km/hour, approximately 15 m above

FIGURE 2 Divisions of King Ranch (left) and an example of aerial survey transects for white-tailed deer on a wildlife management unit (WMU) in South Texas, USA (right), 2011–2015. This WMU contained 3 livestock pastures and each pasture was surveyed independently (thin lines) at 25% coverage (800-m spacing between transects); we pooled results for analysis.

ground level (AGL). Observers count deer out to a visually estimated 91 m on each side of the aircraft. Transects were spaced to cover either 25% (800-m spacing between transects) or 50% (400-m spacing) of each WMU, depending on management objectives. The pilot used a global positioning system (GPS) navigation unit (Garmin Nuvi, Garmin International, Olathe, KS, USA) preloaded with transects created in ArcMap (Esri, Redlands, CA, USA). Observers counted deer and classified individuals by age class (juvenile or adult) and sex (adult male or adult female; DeYoung et al. 1989). They further classified adult (≥1.5 years old) males based on a combination of body characteristics and antler size as either young (1.5–2.5 years old), middle-age (3.5–4.5 years old), or mature (≥5.5 years old). Previous studies using marked deer indicated that experienced observers could place males into these broad age categories with acceptable accuracy (DeYoung et al. 1989). Observers recorded tracklogs and animal detections (group size, sex, and age) within the 182-m swath of the transect using custom CyberTracker applications (CyberTracker Conservation, Cape Town, South Africa) programmed into handheld tablet devices equipped with an internal GPS receiver (Schnupp et al. 2013). After surveys, we combined data stored within tablets for analysis. Surveys for each WMU typically were completed in 1–2 days unless interrupted by inclement weather or mechanical delay.

Data analysis

Observers conducted surveys at the pasture level and we pooled survey results of pastures belonging to the same WMU; thus, we analyzed data for each WMU for each year surveyed (Figure 2). We investigated trends in 3 important demographic ratios (R):

$$\text{juvenile:female, } \hat{R}_{\mathrm{J:F}} = (J_f + J_m)/A_f$$
$$\text{male:female, } \hat{R}_{\mathrm{M:F}} = A_m/A_f$$
$$\text{young:mature male, } \hat{R}_{\mathrm{YM:MM}} = A_{m1-2}/A_{m\geq 3}$$

where J_f, J_m, A_f, and A_m are random variables that represent counts of juvenile females, juvenile males, adult females, and adult males, respectively. For simplicity, we combined the middle-age and mature male age categories and termed both categories as mature ($A_{m\geq 3}$). Thus, the ratio of young:mature males is 1.5–2.5 years old:≥3.5 years old. Further, using the ratio of males 1.5–2.5 years old:≥3.5 years old reflects a situation of surveying for potential changes in male age structures due to chronic wasting disease, where prevalence is typically higher in ≥3.5-year-old males (Miller and Conner 2005, Grear et al. 2006). For each WMU-year survey, we calculated 90% and 95% confidence intervals (CI) for each of the 3 ratios.

There are 2 main approaches to estimate variance of ratio data from a single survey with no marked animals. The Bowden estimator (Bowden et al. 2000) uses differences in ratios among groups of animals encountered during surveys to estimate variation. Because the Bowden estimator uses groups, not individuals, as the sampling unit, the time and effort needed to obtain a reasonable sample size is often too high (Morrison and Kauffman 2014). An alternative method is to use individuals as the sampling unit. For instance, the Czaplewski estimator was developed for estimates of variance for ratio data collected during aerial surveys for mule deer and elk in the western United States (White et al. 2001, Morrison and Kauffman 2014, Monteith et al. 2015). The Czaplewski estimator assumes a normal distribution in ratio data and may not perform well when ratios are skewed; thus, different measures of variance may be more appropriate (Hagen and Loughin 2008). We used log-transformed ratios, $\ln(\hat{R})$, for analysis (Hagen and Loughin 2008, Conner and McKeever 2020) and generated lower and upper CI ($L_{\ln}$, $U_{\ln}$) by first calculating the standard error of each ratio:

$$\mathrm{SE}[\ln(\hat{R}_{J:F})] = \sqrt{\frac{1}{J_f + J_m} + \frac{1}{A_f}}$$

$$\mathrm{SE}[\ln(\hat{R}_{M:F})] = \sqrt{\frac{1}{A_m} + \frac{1}{A_f}}$$

$$\mathrm{SE}[\ln(\hat{R}_{YM:MM})] = \sqrt{\frac{1}{A_{m1-2}} + \frac{1}{A_{m\geq 3}}}$$

then the lower and upper CI, where *r* is the sample ratio:

$$L_{\ln}, U_{\ln} = \ln(r) \pm z_{\alpha/2}\mathrm{SE}[\ln(\hat{R})]$$

where $z_{\alpha/2}$ is the upper α/2 percentile of the standard normal distribution (Hagen and Loughin 2008). We exponentiate to obtain:

$$\mathrm{CI} = [\exp(L_{\ln}), \exp(U_{\ln})].$$

We examined 90% and 95% CIs because management or research objectives may vary and one may opt for a more conservative or strict CI (Czaplewski et al. 1983, Hagen and Loughin 2008).

We generally followed recommendations by Eberhardt (1978), and the British Columbia Terrestrial Ecosystems Task Force (TETFRIC 2002), and defined survey error as the percent difference between the mean and the limits of the confidence interval. We considered surveys to be appropriate for research activities when errors were ≤25%. We considered surveys with errors of ≤50% to be appropriate for a monitoring survey, whereas we classified surveys with >50% errors as uninformative. We calculated frequency of all surveys that produced errors appropriate for research, monitoring, or uninformative surveys for each of the 3 ratios. We also used linear regressions to examine factors that influenced errors of ratio estimates. Error was the response variable, and standardized (mean = 0 and SD = 1) uncorrected deer density (number of deer detected divided by area surveyed, deer/km^2), survey coverage (%), and WMU size (ha) were the predictors. We included year of survey as a factor variable in the model to determine whether error was consistent among years. During 2011–2015, 2012 was a drought year; thus, we used 2012 as the reference level because sample size for juvenile:female ratios could be greatly reduced given the strong association between rainfall and juvenile recruitment (DeYoung et al. 2019). Lastly, we conducted a *post hoc* analysis to evaluate how many ratio-specific detections were needed to meet 25% and 50% errors at 90% and 95% CI. We conducted all analyses and data management in R (R Core Team 2020). Specific R packages included ggplot2 (Wickham 2016), reshape2 (Wickham 2007), dplyr (Wickham et al. 2021), sjPlot (Ludecke 2021), and sjmisc (Ludecke 2018).

RESULTS

We omitted records for 6 WMU-years from analysis because these records appeared to be potential high-leverage outliers: 2 surveys with a high male:female ratio (>2.2), 2 surveys with high young:mature male ratio (>2.5), and 2 surveys when a WMU was flown at 100% coverage. Additionally, 9 WMU-year surveys did not have any detections for either the numerator or the denominator of a ratio, which left us with 177 WMU-year surveys to analyze. Juvenile:female ratios averaged 0.35 (SD = 0.21, range = 0.04–1.10). Average male:female ratio was 0.53 (SD = 0.18, range = 0.13–1.08) and ratio of young to mature males averaged 0.43 (SD = 0.25, range = 0.03–1.56). Detections averaged 1.9 deer/group and uncorrected deer density averaged 6.3 deer/km^2 (SD = 2.4, range = 0.9–13.2). Sizes of WMU averaged 8,161 ha (SD = 3,786, range = 2,749–19,398). Coverage averaged 40.1% (SD = 11.7, range = 15.3–61.7). None of the 3 predictors (coverage, WMU size, and deer density) were strongly correlated (Pearson correlations ≤0.20).

TABLE 1 Mean error (SD), and percent of surveys ($n = 177$) defined as appropriate for monitoring (≤50% error), appropriate for research-based uses (≤25% error), and uninformative (>50% error) for 3 ratios obtained from helicopter surveys of white-tailed deer in 37 wildlife management units during 2011–2015 in South Texas, USA.

CI	Ratio	Error	SD	Monitoring	Research-based	Uninformative
95%	Juvenile:female	0.37	0.13	84	15	16
	Male:female	0.32	0.10	93	27	7
	Young:mature male	0.51	0.15	52	1	48
90%	Juvenile:female	0.33	0.12	90	31	10
	Male:female	0.27	0.09	99	36	1
	Young:mature male	0.45	0.15	69	5	31

At the 95% CI level, ≤27% of ratios were considered to be appropriate for research-based surveys for any demographic measure, whereas the majority of ratios were considered to be appropriate for monitoring surveys (Table 1). Almost half of young:mature male ratios were uninformative.

Distribution of ratio-specific errors were not normal (Shapiro-Wilk normality test $P < 0.01$); thus, we log-transformed errors for each ratio prior to conducting linear regressions to examine factors influencing error. Overall, the results were very similar between models with 90% or 95% CI levels (Figure 3). The standardized predictors in addition to years surveyed explained 82%, 90%, and 80% of the variation in error for juvenile:female, male:female, and young:mature male ratios, respectively. There was an overall trend of WMU size having the largest negative betas (i.e., lower error), followed by uncorrected deer density and survey coverage (Figure 3). At the 95% CI level, 1 standard deviation increase in WMU size (3,782 ha) decreased error in ratios by 17–18% and 1 standard deviation increase in deer density (2.4 deer/km^2) decreased errors by 13–16% (Figure 4). Each unit increase in coverage (1 SD = 11.7%) decreased errors by 11–12%. Relative to year 2012, a drought year, error of male:female and young:mature male ratios were variable among years, whereas juvenile:female ratios consistently had lower error (Figure 5). Errors in juvenile:female ratios were 12–25% lower during non-drought years. *Post hoc* evaluations indicated that at the 95% CI level, 45–60 detections of both groups of a given ratio (e.g., number of male and female detections for male:female ratio) were needed for a monitoring survey, whereas 210–230 detections were needed for a research-based survey (Figure 6). At the 90% CI level, 30–40 and 150–185 detections were needed for monitoring and research-based surveys, respectively (Figure 6).

DISCUSSION

Biologists often implement correction factors or survey methods that account for factors that cause undercounts of population estimates; however, the error of ratio data is rarely considered (Hagen and Loughin 2008). This may be because the effort to acquire acceptable error in ratio data may exceed the effort needed for generating population estimates (Czaplewski et al. 1983). Error is largely a function of sample size, as increases in WMU size, uncorrected deer densities, and coverage all reduced error. Given that a population is decomposed into 2 groups (e.g., juvenile and adult females) or decomposed even further (male age structure), sample size needed for acceptable error in ratio data may be much greater than what is needed for a simple population estimate. Error of demographic ratios is an important consideration given their role in harvest plans and evaluation of the effects of management.

While obtaining 30–40 (90% CI) or 45–60 (95% CI) ratio-specific detections for monitoring surveys were feasible at the ranges of observed coverages and WMU sizes, the error associated with monitoring surveys are not likely to produce detectable changes in ratio data. As a result, it would be difficult to determine the effect of

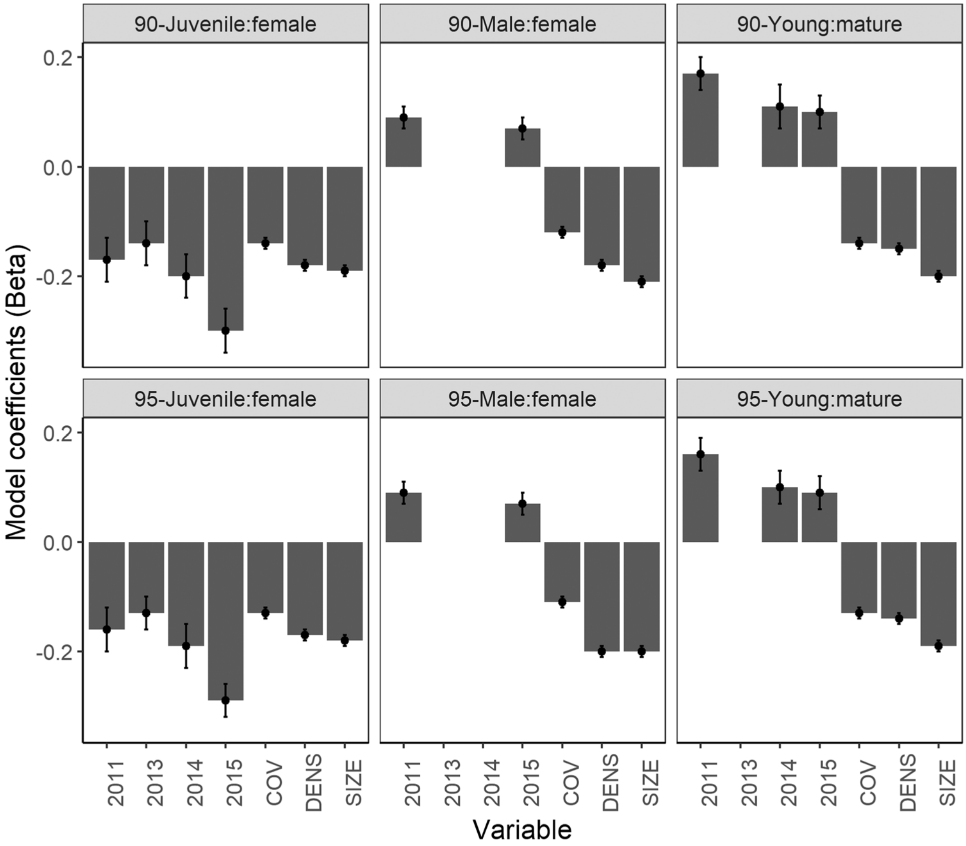

FIGURE 3 Standardized beta coefficients (error bars = SE) from linear regression models examining factors influencing errors at 90% and 95% confidence interval (CI) levels of juvenile:female, male:female, and young:mature male ratios during helicopter surveys of white-tailed deer in 37 wildlife management units in South Texas, USA, 2011–2015. All betas were statistically significant at $P < 0.01$; betas at $P \geq 0.05$ are indicated by absent bars. COV = survey coverage (%), DENS = uncorrected deer density (deer/km^2), and SIZE = size of wildlife management area (ha). We log-transformed ratio data to meet normality assumptions; year 2012 was the reference level.

changes in harvest management or natural mortality. Obtaining sufficient detections of white-tailed deer for research-based surveys may be difficult. White-tailed deer have relatively low detection probabilities (~0.50; DeYoung 1986, Peterson et al. 2020) in southwestern rangelands, likely because of their small group sizes ($\bar{x}$ = 1.9 deer/group, this study). Other ungulates commonly surveyed aerially are more gregarious species that are often surveyed when congregation occurs on winter ranges, resulting in greater detection probability (Table 2). For instance, sightability of elk in Manitoba, Canada was highest during winter compared to other seasons (Vander Wal et al. 2001) and detection probability of elk in South Dakota and Idaho, USA, increased with snow cover and group size (Samuel et al. 1987, Phillips et al. 2019). Researchers have reported that species of ungulates in Tanzania with relatively smaller body sizes and smaller group sizes were more likely to be missed during aerial surveys (Greene et al. 2017).

Compounding the issue of relatively low detection probabilities is that densities of white-tailed deer are relatively lower in southwestern rangelands, generally <30 deer/km^2 (after correcting for visibility and availability bias; DeYoung et al. 1989, Peterson et al. 2020; Figure 1). Densities of white-tailed deer in the more productive midwestern and eastern areas in the United States range from 40–104 deer/km^2 (Walters et al. 2016). Unlike temperate regions, where productive habitat yields higher juvenile recruitment rates and relatively high population densities, the semi-arid environment of South Texas often results in consistently low population densities because of marginally productive habitat combined with variable rainfall (DeYoung 2011). Therefore, it should not be expected for deer densities in southwestern rangelands to appreciably increase to the extent that necessary survey effort would be significantly reduced. Furthermore, extrapolating our findings to the remainder of Texas where

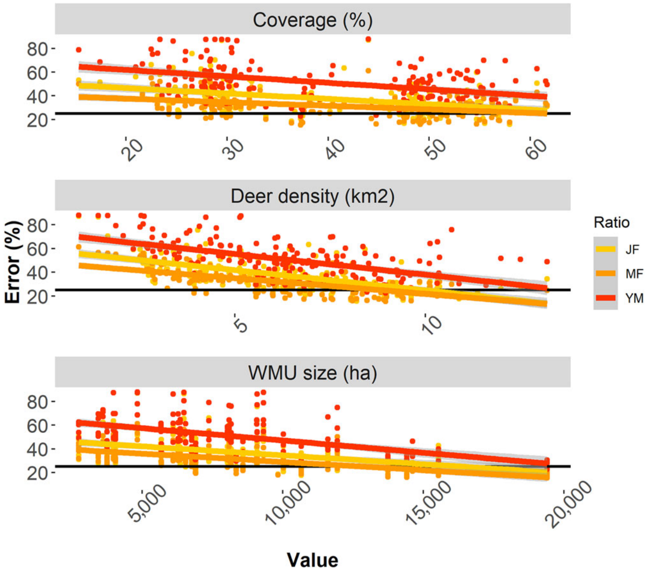

FIGURE 4 Relationship between ratio-specific error (%) and survey coverage, deer density, and wildlife management unit (WMU) size from helicopter surveys for white-tailed deer in South Texas, 2011–2015. JF = juvenile:female ratio, MF = male:female ratio, and YM = young:mature male ratio. Horizontal line indicates error threshold appropriate for research-based surveys (≤25%).

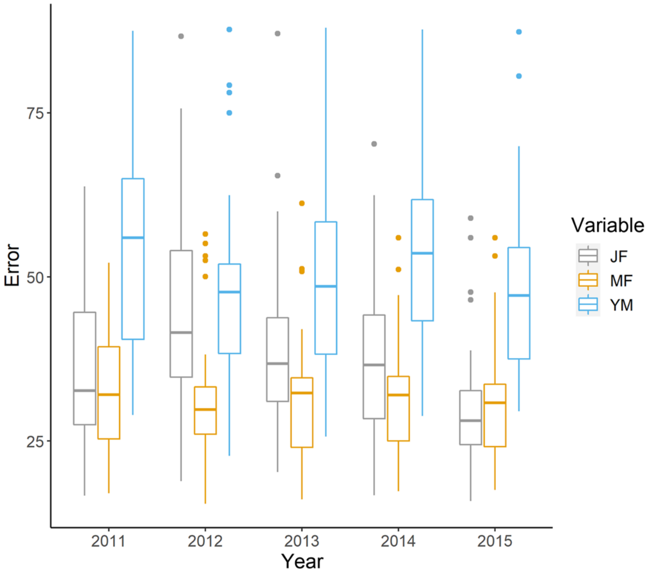

FIGURE 5 Boxplots of errors (%) from 95% confidence intervals (CI) of juvenile:female (JF), male:female (MF), and young:mature male (YM) ratios obtained from helicopter surveys for white-tailed deer in 37 wildlife management units in South Texas, 2011–2015. Average JF error was highest during a drought year (2012) and lowest during a wet year (2015).

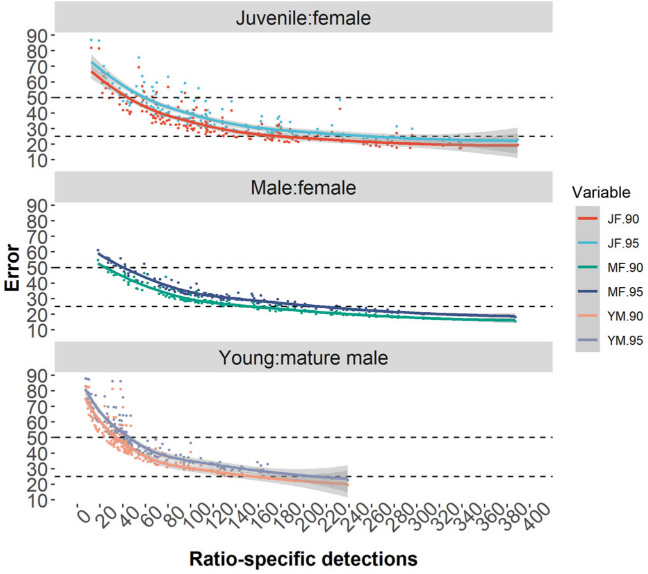

FIGURE 6 Errors of ratio (%) at the 90% and 95% confidence interval level as it related to number of ratio-specific detections obtained during helicopter surveys for white-tailed deer in 37 wildlife management units in South Texas, USA, 2011–2015. JF = juvenile:female, MF = male:female, and YM = young:mature; numbers indicate percent confidence interval level. Horizontal lines indicate error thresholds appropriate for monitoring surveys (≤50%) and research-based surveys (≤25%).

TABLE 2 Detection probabilities (*p*) of ungulate species commonly surveyed during aerial surveys.

Species (scientific name)	*p*	Reference (study area)
Pronghorn (*Antilocapra americana*)	0.64–0.66	Ward (2016) (Texas, USA), Jacques et al. (2014) (South Dakota, USA)
Dall's sheep (*Ovis dalli dalli*)	0.86–0.88	Udevitz et al. (2006) (Alaska, USA)
Moose (*Alces alces*)	0.57–0.69	Peters et al. (2014) (Alberta, Canada)
Elk (*Cervus canadensis*)	0.57–0.61	Samuel et al. (1987) (Idaho, USA), Phillips et al. (2019) (South Dakota, USA)
Mule deer (*Odocoileus hemonius*)	0.11–0.87	Zabransky et al. (2016) (Texas, USA)
White-tailed deer (*O. virginianus*)	0.47–0.55	Peterson et al. (2020) (Texas, USA), DeYoung et al. (1989) (Texas, USA)

aerial surveys are commonly used (Figure 1) indicates that most of Texas, with the exception of the Edwards Plateau and the Cross Timbers ecoregions, will require high survey effort because of comparable deer densities. Coverage can certainly be increased to improve sample sizes but would increase costs and runs the risk of double-counting (Zabransky et al. 2016, but see Beasom et al. 1986).

Juvenile:female ratios, an index of productivity, were often sampled sufficiently to be considered appropriate for monitoring surveys. Error of juvenile:female ratios were consistently lower relative to year 2012, dissimilar with male:female and young:mature male ratios (Figure 3). This pattern likely occurred because of greater variation in juvenile:female ratios, influenced by variable rainfall in this semi-arid environment (Ginnett and Young 2000, Foley et al. 2016). Relatively higher juvenile:female ratios increased sample sizes during wet years (2015), which in turn reduced errors (Figure 5). During drought years (such as 2012), when juvenile recruitment rates are low, additional survey effort will likely be needed to obtain sufficient detections. Furthermore, studies of marked individuals indicated that juvenile white-tailed deer in southwestern rangelands are undercounted by up to 20% relative to adults, likely because of their relatively small body size (Sullivan et al. 1990). The undercount of juveniles indicates additional survey effort may be needed to achieve acceptable errors if one assumed equal detection probabilities.

Errors in juvenile:female ratios are especially important, given that juvenile productivity is often the most critical component explaining population growth for deer (Gaillard et al. 1998). In semi-arid environments, deer populations can be sensitive to additive mortality via harvest (DeYoung 2011, Foley et al. 2016); thus, harvest, particularly of adult females, needs to be conservative. DeYoung et al. (2019) reported that juvenile:female ratios in an experimental study on native southern rangelands that were <0.50 had an apparent population change of <1, indicating a declining population. Therefore, errors in juvenile:female ratios must be sufficient to determine whether a population can be harvested sustainably. Average error was 23% when ≥210 females and juveniles were detected during a survey appropriate for research. Given the average observed juvenile:female ratio of 0.35, a potentially declining population, the 95% CI would be 0.27–0.42, which would allow confirmation that the population likely is not growing. Conversely, average error for monitoring surveys (60–100 detections) was 43%, which would produce a 95% CI of 0.20–0.50. In this case, the upper CI is borderline to a non-declining population, creating difficulties in determining whether the population could absorb female harvest.

Almost all surveys yielded sufficient detections for monitoring male:female ratios; however, fewer male:female ratios had acceptable error for research-based surveys (36% at 90% CI and 27% at 95% CI). Deer managers often strive for a balanced adult sex ratios (Downing 1981). Generally male:female ratios are considered to be balanced when between 0.33–0.50, whereas ratios of ≤0.25 are considered to be skewed (Guynn and Hamilton 1986). With ≥200 detections from a research-based survey, mean male:female ratio (0.53) error was 21% or a 95% CI of 0.42–0.64, which would enable one to determine whether male harvest needs to be adjusted. In the event when sample sizes were appropriate for monitoring surveys (45–100 male and female detections), error averaged 39%. This translates into a 95% CI of 0.32–0.74, which would still allow one to determine whether male:female ratios were skewed but with lower resolution.

The young:mature male ratios required higher effort relative to the other 2 ratios; only 5% (90% CI) or 1% (95% CI) of surveys obtained sufficient samples for a research-based survey because only a few surveys detected ≥210 adult males. Average error of a monitoring survey when 50–100 males were detected during a survey was 40%, which translates into a 95% CI of ±0.17 assuming a mean ratio of 0.43 (95% CI = 0.26–0.60). The wide CI overlaps both a mature-biased and young-biased male age structure. The high error of young:mature males indicates that survey effort will have to be very high, perhaps too high given the potential for male age misclassification (Leon et al. 1987, Shupe and Beasom 1987, Bender et al. 2003, Conner and McKeever 2020). The relatively high error of male age structure ratio is a consideration for evaluating effectiveness of management strategies designed to increase male survivorship into older age classes (Bender and P. J. Miller 1999, Wallingford et al. 2017). Further, chronic wasting disease has a disproportionate impact on older males, which has caused agencies to monitor age structure as it relates to disease prevalence (Conner et al. 2021). Suppose chronic wasting disease increased mortality of the mature male population by 10%, the mean ratio of young:mature male would change from 0.43 to 0.48; the average error of 40% (95% CI = 0.26–0.60) from a monitoring survey would not allow detection of the change in the male age structure. Therefore, using helicopter surveys in southwestern rangelands may not be the best approach to detect effects of the disease on male age structures, as it would be difficult to detect significant changes.

In southwestern rangelands, search effort needed to monitor juvenile:female and male:female ratios, but not young:mature males, via autumn helicopter surveys was reasonable given that 30–60 detections of each ratio-specific group were largely achievable with 25–50% coverage at the WMU scale. Coincidentally, obtaining 30–60 ratio-specific detections would likely be sufficient to generate population estimates via distance sampling (Buckland et al. 2015, Peterson et al. 2020) because the sum of all 3 sex-age classes (juveniles, females, and males) would likely be >60–80 detections. Achieving ratio data with ≤25% error would be difficult at the observed WMU sizes at 25–50% coverage. Therefore, multi-year trend analyses would be more appropriate to examine changes in ratio data instead of making conclusions from a single survey (DeYoung et al. 1989). Alternatively, conducting repeated aerial surveys may be a more viable approach because variation could be computed from the repeated estimates of the ratios themselves; total flying time of repeated surveys may be less than a single high-effort survey (Beasom et al. 1986), which would reduce total costs; and repeated surveys can be conducted with relatively low coverages (Beasom et al. 1986), which may reduce concerns of double-counting at high coverages. Our findings that acceptable error would require relatively high effort also has implications for quantifying changes in demographic ratio data at smaller scales. Field studies evaluating the effect of cattle grazing, local precipitation, or prescribed burns on demographic ratios will likely have to use alternative survey methods that generate sufficient samples for satisfactory error.

Although the variation in demographic ratios has long been appreciated (Czaplewski et al. 1983), our results highlight the lack of information regarding error of survey-generated ratio data in the scientific literature emphasized by previous studies (Hagen and Loughin 2008). Overall, reporting variation in ratio data from aerial surveys appears to be species-specific; variation is commonly reported for gregarious species rather than species that occur in small groups. This tendency likely occurs because a high proportion of the population of gregarious species can be simultaneously sighted in a defined area (Bender et al. 2003, Citta et al. 2014), such as elk or mule deer at winter grounds or aggregations of marine mammals (e.g., hauled-out Pacific walrus [*Odobenus rosmarus*]). The error of ratio data appears to be better appreciated for species of upland birds, where other means of population estimates are often unavailable (Hagen and Loughin 2008).

Ultimately, it is up to the manager or researcher how much effort to spend collecting ratio data given there is a trade-off in time and money versus variance of ratio data. Some authors have suggested that funds spent towards conducting aerial surveys may be better spent elsewhere (Thomas 1998, Urbanek et al. 2012, Collier et al. 2013). The combination of different sources of information into an integrated population model offers an alternative approach to monitoring that appears promising for low-density populations (Moeller et al. 2021). Regardless, managers and scientists should quantify error of their demographic estimates to ensure that appropriate management decisions are being made because errors will likely be site-specific.

MANAGEMENT IMPLICATIONS

Error in ratio data obtained from helicopter surveys of white-tailed deer in South Texas often did not have sufficient power to detect meaningful changes. Furthermore, young:mature male ratios had the highest errors relative to juvenile:female and male:female ratios. Therefore, modifying survey protocol, such as increasing survey coverage to increase number of deer detections, would reduce errors. With the emergence of chronic wasting disease in South Texas and elsewhere, generating acceptable errors in ratio data will play an important role in understanding effects on population dynamics. For instance, given the high error in young:mature male ratios, it will be very difficult to use helicopter surveys to monitor changes in male age structures due to chronic wasting disease at our observed deer densities. We encourage managers to quantify and report errors to ensure that correct inferences are made on the demographic ratio data. Our approach of evaluating errors can easily be used as a guideline by other managers to determine how much survey effort is needed to obtain sufficient detections based on area-specific deer densities and detection probabilities.

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CONFLICTS OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

This study did not involve capture or handling of animals.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

Adams, K. P., and R. J. Hamilton. 2011 Management history. Pages 368–391 *in* D. G. Hewitt, editor. Biology and management of white-tailed deer. CRC Press, Boca Raton, Florida, USA.

Barker, R. 2008. Theory and application of mark-recapture and related techniques to aerial surveys of wildlife. Wildlife Research 35:268–274.

Beasom, S. L., F. G. Leon, and D. R. Synatzske. 1986. Accuracy and precision of counting white-tailed deer with helicopters at different sampling intensities. Wildlife Society Bulletin 14:364–368.

Bender, L. C. 2006. Uses of herd composition and age ratios in ungulate management. Wildlife Society Bulletin 34:1225–1230.

Bender, L. C., and P. J. Miller. 1999. Effects of elk harvest strategy on bull demographics and herd composition. Wildlife Society Bulletin 27:1032–1037.

Bender, L. C., W. L. Myers, and W. R. Gould. 2003. Comparison of helicopter and ground surveys for North American elk *Cervus elaphus* and mule deer *Odocoileus hemionus* population composition. Wildlife Biology 9:199–205.

Beringer, J, L. P. Hansen, and O. Sexton. 1998. Detection rates of white-tailed deer with a helicopter over snow. Wildlife Society Bulletin 26:24–28.

Bleich, V. C., R. T. Bowyer, A. M. Pauli, M C. Nicholson, and R. W. Anthes. 1994. Mountain sheep *Ovis canadensis* and helicopter surveys: ramifications for the conservation of large mammals. Biological Conservation 70:1–7.

Biederbeck, H. H., M. C. Boulay, and D. H. Jackson. 2001. Effects of hunting regulations on bull elk survival and age structure. Wildlife Society Bulletin 29:1271–1277.

Bowden, D. C., G. C. White, and R. M. Bartmann. 2000. Optimal allocation of sampling effort for monitoring a harvested mule deer population. Journal of Wildlife Management 64:1013–1024.

Bowyer, R. T., V. C. Bleich, K. M. Stewart, J. C. Whiting, and K. L. Monteith. 2014. Density dependence in ungulates: a review of causes, and concepts with some clarifications. California Fish and Game 100:550–572.

Buckland, S. T., E. A. Rexstad, T. A. Marques, and C. S. Oedekoven. 2015. Distance sampling: Methods and applications. Springer, New York, New York, USA.

Caughley, G. 1977. Sampling in aerial survey. Journal of Wildlife Management 41:605–615.

Citta, J. J., L. T. Quackenbush, and B. D. Taras. 2014. Estimation of calf:cow ratios of Pacific walruses for use in population modeling and monitoring. Marine Mammal Science 30:20–43.

Cochran, W. G. 1977. Sampling techniques. Wiley, New York, New York, USA.

Collier, B. A., S. S. Ditchkoff, C. R. Ruth, Jr., and J. B. Raglin. 2013. Spotlight surveys for white-tailed deer: monitoring panacea or exercise in futility? Journal of Wildlife Management 77:165–171.

Conner, M. M., and J. S. McKeever. 2020. Are composition surveys for mule deer along roads or from helicopters biased? Lessons from the field. Wildlife Society Bulletin 44:142–151.

Conner, M. M., M. E. Wood, A. Hubbs, J. Binfet, A. A. Holland, L. R. Meduna, A. Roug, J. P. Runge, T. D. Nordeen, M. J. Pybus, and M. W. Miller. 2021. The relationship between harvest management and chronic wasting disease prevalence trends in western mule deer (*Odocoileus hemionus*) herds. Journal of Wildlife Diseases 57:831–843.

Czaplewski, R. L., D. M. Crowe, and L. L. McDonald. 1983. Sample sizes and confidence intervals for wildlife population ratios. Wildlife Society Bulletin 11:121–128.

DeVivo, M. T., D. R. Edmunds, M. J. Kauffman, B. A. Schumaker, J. Binefet, T. J. Kreeger, B. J. Richards, H. M. Schatzl, and T. E. Cornish. 2017. Endemic chronic wasting disease causes mule deer population decline in Wyoming. PloS ONE 12(10):e0186512.

DeYoung, C. A. 1985. Accuracy of helicopter surveys of deer in South Texas. Wildlife Society Bulletin 13:146–149.

DeYoung, C. A. 2011. Population dynamics. Pages 311–351 *in* D. G. Hewitt, editor. Biology and management of white-tailed deer. CRC Press, Boca Raton, Florida, USA.

DeYoung, C. A., T. E. Fulbright, D. G. Hewitt, D. B. Wester, and D. A. Draeger. 2019. Linking white-tailed deer density, nutrition, and vegetation in a stochastic environment. Wildlife Monographs 202:1–63.

DeYoung, C. A., F. S. Guthery, S. L. Beasom, S. P. Coughlin, and J. R. Heffelfinger. 1989. Improving estimates of white-tailed deer abundance from helicopter surveys. Wildlife Society Bulletin 17:275–279.

DeYoung, C. A., J. R. Heffelfinger, S. L. Beasom, and S. P. Coughlin. 1989. Classifying male white-tailed deer from a helicopter. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 43:292–296.

DeYoung, R. W., and K. V. Miller. 2011. White-tailed deer behavior. Pages 324–367 *in* D. G. Hewitt, editor. Biology and management of white-tailed deer. CRC Press, Boca Raton, Florida, USA.

Downing, R. L. 1981. Deer harvest sex ratios: a symptom, a prescription, or what? Wildlife Society Bulletin 9:8–13.

Eberhardt, L. L. 1978. Appraising variability in population studies. Journal of Wildlife Management 42:207–238.

Foley, A. M., D. G. Hewitt, C. A. DeYoung, R. W. DeYoung, and M. J. Schnupp. 2016. Modeled impacts of chronic wasting disease on white-tailed deer in a semi-arid environment. PLoS ONE 11:e0163592.

Foley, A. M., J. S. Lewis, O. Cortez, M. W. Hellickson, D. G. Hewitt, R. W. DeYoung, C. A. DeYoung, and M. J. Schnupp. 2022. Accuracies and biases of ageing white-tailed deer in semiarid environments. Wildlife Research 49:237–249.

Freddy, D. J., G. C. White, M C. Kneeland, R. H. Kahn, J. W. Unsworth, W. J. deVergie, V. K. Graham, J. H. Ellenberger, and C. H. Wagner. 2004. How many mule deer are there? Challenges of credibility in Colorado. Wildlife Society Bulletin 32:916–927.

Frenette, J, F. Pelletier, and M. H. St. Laurent. 2020. Linking habitat, predators, and alternative prey to explain recruitment variations of an endangered caribou population. Global Ecology and Conservation 22:e00920.

Fulbright, T. E., and J. A. Ortega-S. 2006. White-tailed deer habitat: ecology and management on rangelands. Texas A&M University Press, College Station, USA.

Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58–63.

Gasaway, W. C., S. S. DuBois, D. J. Reed, and S. J. Harbo. 1986. Estimating moose population parameters from aerial surveys. Biological Papers 22. University of Alaska, Fairbanks, USA.

Ginnett, T. F., and E. L. B. Young. 2000. Stochastic recruitment in white-tailed deer along an environment gradient. Journal of Wildlife Management 64:713–720.

Ginsberg, J. R., and E. J. Milner-Gulland. 1994. Sex-biased harvesting and population dynamics in ungulates: implications for conservation and sustainable use. Conservation Biology 8:57–166.

Grear, D. A., M. D. Samuel, J. A. Langenberg, and D. Keane. 2006. Demographic patterns and harvest vulnerability of chronic wasting disease infected white-tailed deer in Wisconsin. Journal of Wildlife Management 70:546–553.

Greene, K., D. Bell, J. Kioko, and C. Kiffner. 2017. Performance of ground-based and aerial survey methods for monitoring wildlife assemblages in a conservation area of northern Tanzania. European Journal of Wildlife Research 63:1–13.

Griffith, G. E., S. A. Bryce, J. M. Omernik, J. A. Comstock, A. C. Rogers, B. Harrison, S. L. Hatch, and D. Bezanson. 2004. Ecoregions of Texas. U.S. Geological Survey (map scale 1:2,500,000), Reston, Virginia, USA.

Guynn, D. C., and R. J. Hamilton. 1986. The effects of adult sex ratio on reproduction in white-tailed deer. Pages 233–240 *in* Proceedings of the International Ranchers Roundup. Texas Agricultural Research and Extension Center, 18–21 August 1986, College Station, USA.

Hagen, C. A., and T. M. Loughin. 2008. Productivity estimates from upland bird harvests: estimating variance and necessary sample sizes. Journal of Wildlife Management 72:1369–1375.

Hansen, L. 2011. Extensive management. Pages 409–451 *in* D. G. Hewitt, editor. Biology and management of white-tailed deer. CRC Press, Boca Raton, Florida, USA.

Hansen, L. P., E. B. Flinn, J. A. Sumners, X. Gao, and J. J. Millspaugh. 2017. Effects of an antler point restriction on deer hunter perceptions and satisfaction in Missouri. Wildlife Society Bulletin 41:516–522.

Heffelfinger, J. R. 2011. Taxonomy, evolutionary history, and distribution. Pages 3–39 *in* D. G. Hewitt, editor. Biology and management of white-tailed deer. CRC Press, Boca Raton, Florida, USA.

Islam, M. R., U. Bulut, T. P. Feria-Arroyo, M. G. Tyshenko, and T. Oraby. 2022. Modeling the impact of climate change on cervid chronic wasting disease in semi-arid South Texas. Frontiers in Epidemiology 2:889280.

Jacques, C. N., J. A. Jenks, T. W. Grovenburg, R. W. Klaver, and C. S. DePerno. 2014. Incorporating detection probability into northern Great Plains pronghorn population estimates. Journal of Wildlife Management 78:164–174.

Larter, N. C., T. S. Jung, and D. G. Allaire. 2017. Snow depth does not affect recruitment in a low-density population of boreal woodland caribou (*Rangifer tarandus*). European Journal of Wildlife Research 61:1–4.

Leon, F. G., III, C. A. DeYoung, and S. L. Beasom. 1987. Bias in age and sex composition of white-tailed deer observed from helicopters. Wildlife Society Bulletin 15:426–429.

Ludecke, D. 2018. sjmisc: data and variable transformation functions. Journal of Open Source Software 26:754.

Ludecke, D. 2021. sjPlot: data visualization for statistics in social science. R package version 2.8.10. <https://CRAN.R-project.org/package=sjPlot>

Miller, M. W., and M. M. Conner. 2005. Epidemiology of chronic wasting disease in free-ranging mule deer: spatial, temporal, and demographic influences on observed prevalence patterns. Journal of Wildlife Diseases 41:275–290.

Moeller, A. K., J. J. Nowak, L. Neufeld, M. Bradley, M. Manseau, P. Wilson, S. McFarlane, P. M. Lukacs, and M. Hebblewhite. 2021. Integrating counts, telemetry, and non-invasive DNA data to improve demographic monitoring of an endangered species. Ecosphere 12:e03443.

Monteith, K. L., R. W. Klaver, K. R. Hersey, A. A. Holland, T. P. Thomas, and M. J. Kauffman. 2015. Effects of climate and plant phenology on recruitment of moose at the southern extent of their range. Oecologia 178:1137–1148.

Morrison, T. A., and M. J. Kauffman. 2014. Mule deer modeling report. Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, USA.

Mysterud, A., P. Hopp, K. R. Alvseike, S. L. Benestad, E. B. Nilsen, C. M. Rolandsen, O. Strand, J. Vage, and H. Viljugrein. 2020. Hunting strategies to increase detection of chronic wasting disease in cervids. Nature Communications 11:1–11.

National Oceanic and Atmospheric Administration [NOAA]. 2021. NOAA National Centers for Environmental Information, climate at a glance: county mapping. <https://www.ncdc.noaa.gov/cag/>. Accessed 8 Aug 2021.

Norwinen, J., and K. John. 2007. The changing climate of South Texas, 1900–2100: problems and prospects, impacts and implications. BookMasters, Ashland, Ohio, USA.

Parent, C. J., F. Hernández, L. A. Brennan, D. B. Wester, F. C. Bryant, and M. Schnupp. 2016. Northern bobwhite abundance in relation to precipitation and landscape structure. Journal of Wildlife Management 80:7–18.

Peters, W., M. Hebblewhite, K. G. Smith, S. M. Webb, N. Webb, M. Russell, C. Stambaugh, and R. B. Anderson. 2014. Contrasting aerial moose population estimation methods and evaluating sightability in west-central Alberta, Canada. Wildlife Society Bulletin 38:639–649.

Peterson, M. K., A. M. Foley, A. N. Tri, D. G. Hewitt, R. W. DeYoung, C. A. DeYoung, and T. A. Campbell. 2020. Mark-recapture distance sampling for aerial surveys of ungulates on rangelands. Wildlife Society Bulletin 44: 713–723.

Phillips, E. C., C. P. Lehman, R. W. Klaver, A. R. Jarding, S. P. Rupp, J. A. Jenks, and C. N. Jacques. 2019. Evaluation of an elk detection probability model in the Black Hills, South Dakota. Western North American Naturalist 79: 551–565.

Pollock, K. H., H. D. Marsh, I. R. Lawler, and M. W. Alldredge. 2006. Estimating animal abundance in heterogenous environments: an application to aerial surveys for dugongs. Journal of Wildlife Management 70:255–262.

Potvin, F., L. Breton, and L. P. Rivest. 2004. Aerial surveys for white-tailed deer with the double-count technique in Quebec: two 5-year plans completed. Wildlife Society Bulletin 32:1099–1107.

R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ricklefs, R. E. 1997. Comparative demography of New World populations of thrushes (*Turdus* spp.) Ecological Monographs 67:23–43.

Sæther, B. E., E. J. Solberg, and M. Heim. 2003. Effects of altering sex ratio structure on the demography of an isolated moose population. Journal of Wildlife Management 67:455–466.

Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys of elk in Northcentral Idaho. Journal of Wildlife Management 51:622–630.

Samuel, M. D., and K. H. Pollock. 1981. Correction of visibility bias in aerial surveys where animals occur in groups. Journal of Wildlife Management 54:993–997.

Schnupp, M. J., F. Hernández, E. J. Redeker, F. C. Bryant, J. P. Rusk, S. J. DeMaso, J. P. Sands, T. W. Teinert, L. A. Brennan, D. Rollins, and R. M. Perez. 2013. An electronic system to collect distance-sampling data during helicopter surveys of northern bobwhite. Wildlife Society Bulletin 37:236–245.

Shupe, T. E., and S. L. Beasom. 1987. Speed and altitude influences on helicopter surveys of mammals in brushland. Wildlife Society Bulletin 15:552–555.

Sullivan, J. B., C. A. DeYoung, S. L. Beasom, J. R. Heffelfinger, S. P. Coughlin, and M. W. Hellickson. 1990. Evaluation of bias in the proportion of white-tailed deer fawns sighted from helicopters. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies. 44:202–205.

Terrestrial Ecosystems Task Force Resources Inventory Committee [TETFRIC]. 2002. Aerial-based inventory methods for selected ungulates: bison, mountain goat, mountain sheep, moose, elk, deer and caribou. https://www.arlis.org/docs/vol1/Q/50842282.pdf. Accessed 15 Nov 2021.

Texas Parks and Wildlife Department. 2022. New chronic wasting disease surveillance, containment zones proposed in five counties. <https://tpwd.texas.gov/newsmedia/releases/?req=20220805a>. Accessed 5 Aug 2022.

Thomas, D. 1998. Needed: less counting of caribou and more ecology. Rangifer 10:15–23.

Udevitz, M. S., B. S. Shults, L. G. Adams, and C. Kleckner. 2006. Evaluation of aerial survey methods for Dall's sheep. Wildlife Society Bulletin 34:732–740.

Uehlinger, F. D., A. C. Johnston, T. K. Bollinger, and C. L. Waldner. 2016. Systematic review of management strategies to control chronic wasting disease in wild deer populations in North America. BMC Veterinary Research 12:1–16.

Urbanek, R. E., C. K. Nielsen, T. S. Preuss, and G. A. Glowacki. 2012. Comparison of aerial surveys and pellet-based distance sampling methods for estimating deer density. Wildlife Society Bulletin 36:100–106.

Vander Wal, E., P. D. McLoughlin, and R. K. Brook. 2001. Spatial and temporal factors influencing sightability of elk. Journal of Wildlife Management 75:1521–1526.

Wallingford, B. D., D. R. Diefenbach, E. S. Long, C. S. Rosenberry, and G. L. Alt. 2017. Biological and social outcomes of antler point restriction harvest regulations for white-tailed deer. Wildlife Monographs 196:1–26.

Walters, B. F., C. W. Woodall, and M. B. Russell. 2016. White-tailed deer density estimates across the eastern United States, 2008. Data Repository for the University of Minnesota, Minneapolis, USA. https://doi.org/10.13020/D6G014

Ward, C. L. 2016. Evaluation of survey techniques and sightability for pronghorn antelope (*Antilocapra americana*) in Texas. Thesis, Texas A&M University-Kingsville, Kingsville, USA.

White, G. C., D. J. Freddy, R. B. Gill, and J. H. Ellenberger. 2001. Effect of adult sex ratio on mule deer and elk productivity in Colorado. Journal of Wildlife Management 65:543–551.

Wickham, H. 2007. Reshaping data with the reshape package. Journal of Statistical Software 21:1–20.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis. Springer-Verlag, New York, New York, USA.

Wickham, H., R. Francois, L. Henry, and K. Muller. 2021. dplyr: a grammar of data manipulation. R package version 1.0.6. https://CRAN.R-project.org/package=dplyr

Williams, E. S., M. W. Miller, T. J. Kreeger, R. H. Kahn, and E. T. Thorne. 2002. Chronic wasting disease of deer and elk: a review with recommendations for management. Journal of Wildlife Management 66:551–563.

Zabransky, C. J., D. G. Hewitt, R. W. DeYoung, S. Gray, C. Richardson, A. R. Litt, and C. A. DeYoung. 2016. A detection probability model for aerial surveys of mule deer. Journal of Wildlife Management 80:1379–1389.

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