ECOLOGY OF SYMPATRIC DEER SPECIES IN WEST-CENTRAL TEXAS: METHODOLOGY, REPRODUCTIVE BIOLOGY, AND MORTALITY AND ANTIPREDATOR STRATEGIES OF ADULT FEMALES AND FAWNS

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I would also like to thank God and Satan. God provided us with this wonderful world in the cosmic environment and blessed us with the marvelous process we termed evolution. It is by evolution that we and all else exist, and it should be somewhat comforting to know that evolution needs no day of rest and will never stop; the hand of God is always present. In contrast, Satan provides job security for us wildlife professionals by way of exponential growth in the human population and ever increasing pollution, climate change, and wildlife-human conflicts; more land is needed to feed

more people, which produces more people that need more land, and you see the trend. The Earth's supply of natural resources and services decreases as our demand simultaneously increases. Satan wants us to destroy ourselves and the rest of evolution's natural beauty, and his best tools seem to be politics and religion; it is quite obvious that these are the two most blinding forces for humans, but even they are understandable in an evolutionary context. You have to admit, Satan makes life interesting, but if we want to thwart our destructive natural instincts, the only viable path I can see is ecological education from grades K–12 (e.g., natural and sexual selection, phylogeny and ontogeny, extinction, animal behavior, population dynamics, community relationships, disturbance theory, island biogeography, ecological services, etc.). Perhaps if people had just a basic but sound understanding of life on Earth, they would care enough and be inspired to think independently. In our free society, it is only the majority that will make the required difference. We are different from all other taxa because *Homo sapiens* is the only species able to mourn the loss of another (see Leopold), capable of both biophilic altruism and group selection as we understand it; the majority just need to chose it. It is the struggle against Satan that brings out the best in those people who can see through the guise.

I dedicate this work to Milan, a true and gentle friend that really liked rabbits, opposums, skunks, porcupines, tarantulas, javelinas, huskies, and deer fawns, but not so much parakeets or kittens, which were just too darn scary. I am not sure where Schipperkes fit into that list, but I suspect you were mostly just tolerant for our benefit – perhaps the only other species on Earth capable of regular altruism, *Canis domesticus*. You will be missed as long as Alicia or I live.

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ABSTRACT

Between the mid-1800s and -1900s mule deer (*Odocoileus hemionus*) declined to relict populations in west Texas. This event coincided with the advent of barbed-wire fencing and dug wells providing water by windmills, which brought an end to free-ranging livestock. Also coincident was rangeland conversion from grassland-savannah to more brush dominated habitats due to overgrazing and fire suppression. These conditions favored white-tailed deer (*O. virginianus*) that expanded their range westward with the brush into areas that were previously inhabited by mule deer only. Most local biologists would cite the west-Texas decline of mule deer as the result of unfavorable changes in rangeland habitats, which facilitated competitive exclusion by white-tailed deer. Others have speculated about effects of fragmentation and hybridization, although genetic introgression between deer species appears uncommon despite hybridization in sympatric contact zones. However, these conditions still exist in west Texas, and mule deer are making their comeback into their previous range that was only occupied by white-tailed deer 30 years ago. The question remains: why did mule deer disappear 100 years ago? We think we have the answer: diseases associated with livestock.

To reach that overarching conclusion (as a hypothesis), we first: 1) refined our field methods, 2) studied reproductive biology, and 3) examined causes of death for adult females and fawns of both species in a contact zone in northwest Crockett County, Texas, an area that was inhabited only by mule deer 100 years ago and only by white-tailed deer 30 years ago. They are now of similar abundance. We also made a discovery regarding maternal antipredator strategies that seems interesting for both ecology and management.

I will not expound here on detailed results, as each chapter has its own abstract of more appropriate form.

Because we relied on deer location estimates by radiotelemetry to test hypotheses, I conducted a beacon study to determine errors and generate a predictive regression model. This model allowed me to assess whether or not objectives could be met given our field methods. I also created a common-sense approach to location estimation that incorporated subjective weighting by relative confidence in a signal received. I compared this approach to the commonly used maximum likelihood estimator. Other researchers may find my MATLAB files useful for beacon studies and location estimation by radiotelemetry triangulation (see http://www.rw.ttu.edu/haskell/).

To interpret results from wildlife studies it is useful to know population densities. We used mark-resight and deer location data to generate a theoretically unbiased deer density estimate at our site in 2005 (approx. 30 deer/km^2). We took advantage of this estimate to provide Texas Parks and Wildlife Department (TPWD) with the first scientifically valid field assessment of their deer survey methods from roads. As predicted, because of habituation behavior within (and perhaps beyond) the effective survey strip width, deer seemed to be clustered near roads as semi-permeable barriers to movement, although a displacement effect of approximately 30 m was also evident. We provided TPWD with recommendations to calibrate their non-random survey design to more defensible methods.

Field methods for fawn studies have been continuously refined. Most prior studies suffered from potential positive survival biases because fawns were not captured as true neonates and survival rates may be lowest soon after birth. In fact, 9% of the fawns we captured died within 25 m of birth-sites; most of these were not handled prior to death. We agree with others that risk of marking-induced abandonment is low if females are allowed at least 3 hours postpartum to clean and nurse their young. We used vaginal implant transmitters (VITs) to locate birth-sites. We experimented with VIT design to determine variable efficacy. Despite previous behavioral observations from captive deer, we found that antennas protruding too far externally from the vulva were more likely to be prematurely expelled, presumably because deer pulled them out with their teeth. Also we found that previous models estimating ages of captive fawns by hoof growth predicted ages that were about 1.5 weeks too young for our free-ranging fawns. Thus, researchers should take considerable caution when applying models from captive deer to free-ranging populations. We found that white-tailed deer moved neonates farther faster from birth-sites than did mule deer females. We hypothesized that this observed phenomenon was due to differences in maternal antipredator strategies, to be discussed more later.

I examined factors affecting birth dates of these sympatric species at 3 hierarchal levels. At the population level, white-tailed deer birthed 1 month earlier than mule deer, and both species birthed later when rain was reduced during the pre-rut and rut periods. We suggest that the different birthing (and presumably breeding) periods for these sympatric species was not the result of selective pressure against hybridization, but instead was the result of some degree of phylogenetic constraint from parent populations. That is, the white-tailed deer expanded from central Texas where birthing is in mid-June, whereas the mule deer (*O. h. eremicus*) originated from southwestern deserts where birthing is synchronized with convective rain storms later in summer. At the individual level, older and heavier females birthed earlier. Reproductive success from the previous year may have greater effect on timing of breeding and birthing at other sites than at our study site because females seemed to invest relatively little energy in rearing fawns at our site. Also, deer birthed later on the more overgrazed ranches, suggesting an inter-generational effect after other factors were accounted for in multiple regression.

This deer herd likely exists near a K-carrying capacity that responds positively to rain. As predicted, white-tailed adult females survived better during a period of greater rain than during drought. Unexpectedly, mule deer females that had nearly 100% survival during drought had reduced survival 2 years after the substantial rains of 2004. We hypothesize that the rains of 2004 directly and indirectly created an environment more favorable for disease transmission. Reproductive rates were high for both species, but were reduced in 2006 following reduced rain in the pre-rut and rut period of 2005, although mule deer females may have been stressed for the reason previously cited. Hemorrhagic diseases were chronically endemic in both species, but white-tailed deer are thought to have previously obtained enzootic stability in Texas. Overall, mule deer fawns succumbed more to sickness and starvation, and white-tailed fawns were killed more by bobcats (*Lynx rufus*). Even in 2004, one of the wettest summers in west Texas history, sickness-starvation was the biggest killer of mule deer fawns. Apparent diseases were numerous, and diseases associated with domestic sheep may have been more pathogenic than those associated with cattle. Mule deer kept fawns nearby and close together to protect them from seemingly overabundant small predators (e.g., bobcats and foxes), in the absence of larger predators such as coyotes (*Canis latrans*). In contrast, white-tailed females separated fawns and were generally removed from them during the

fawn hider phase, 3 weeks postpartum. Given the long evolutionary history of white-tailed deer with many large predators, this loose cohesion antipredator strategy may be adaptive in the presence of large predators, but was maladaptive in their absence because extirpation of large predators can release populations of smaller predators that could be defended against. While bobcats tended to kill healthy fawns, bobcat predation may be to some degree compensatory, as the only appreciable top-down limiting factor on this deer herd, if the long-term effect is to alleviate negative density-dependent consequences of life near K-carrying capacity.

Data from adult female weights and survival and fawn survival, thymus glands, weight gain, new hoof growth, birth dates, and weaning dates indicated that this deer population was chronically stressed near a carrying capacity that fluctuated with rain, and that females invested relatively energy in rearing fawns. We suggest that it was pathogens introduced by livestock ranchers that were responsible for the historic decline of a naïve mule deer herd in west Texas. Mule deer appear to have developed some immunity and may eventually achieve enzootic stability similar to white-tailed deer. Human use of these private lands and the unhealthy deer herd has been consistent for decades and likely will remain so. Responsible deer management is impossible where human land-use practices affect ecology and demographics across fence-lines and top-down limitation is negligible. We recommend research into alternative economic means and public ecological education of youth and adults as the management action with greatest potential for desirable results.

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CHAPTER I

INTRODUCTION

Introducing the past, current, and future state of our understanding of deer ecology and management is no small task. It requires a good deal of space and a whole lot of literature cited. Because I have done so in each of the following individual chapters in accordance with the subject matter, I will not be repetitive here. Texas Parks and Wildlife Department (TPWD) contracted the Texas Tech University Department of Natural Resources Management, with project leadership under Dr. Warren Ballard, to investigate cause-specific fawn mortality in a sympatric population of white-tailed deer (*Odocoileus virginianus*) and desert mule deer (*O. hemionus eremicus*) located in northwest Crockett County, Texas. We did that and more. We: 1) developed a new technique for radiotelemetry and provided useful Matlab code for beacon studies and triangulation location estimation by weighted-incenter or maximum likelihood methods (http://www.rw.ttu.edu/haskell), 2) provided TPWD with the first critical and scientifically valid field-assessment of their deer survey methods from roads, 3) refined methods for capturing and aging deer fawns while raising awareness of the dangers in extrapolating results from captive studies to free-ranging populations, 4) examined environmental influences, including anthropogenic sources, on reproductive biology, 5) examined adult female survival, 6) examined significance and patterns of fawn mortality, and 7) examined postpartum maternal antipredator strategies between species. As in most wildlife ecology, the devil is in the details, and we build cases with multiple lines of evidence as much as possible. We discussed implications for ecology, management, and research.

Our research was observational, but we formed *a priori* hypotheses and predictions as much as possible to be conducive to the hypothetico-deductive approach to science. Thus, rather than assuming a constant environment in a treatment and non-treatment study design (i.e., no such thing as a "control" at these spatial and temporal scales), we relied on the variable environment to provide conditions for natural experiments. This worked better than may be expected, and multiple regression was the analytical tool of choice and the best way to control potential variables, contingent on measurement error. With the benefit of improved technologies and careful attention to methodology, we were able to answer questions (and forward new ones) regarding deer ecology and management that were previously mostly speculative. Inferences are most often limited in scope to the spatial and temporal extent of our study.

The following chapters constitute partial fulfillment of the requirements of Doctor of Philosophy in Wildlife Science for the Graduate School at Texas Tech University. Each is a manuscript for scientific publication. For consistency they have been formatted in the style of a *Wildlife Monograph* manuscript with some modification as required by the Graduate School.

Chapter II is titled: "Accounting for radiotelemetry signal flux in triangulation point estimation." Authors are Shawn P. Haskell and Warren B. Ballard. This manuscript was published in 2007 in the *European Journal of Wildlife Research* 53:204–211.

Chapter III is titled: “Deer density estimation in west-central Texas: old versus new ground techniques with mark-resight as a comparative baseline.” Authors are Shawn P. Haskell, David A. Butler, Warren B. Ballard, Matthew J. Butler, Mark C. Wallace, and Mary H. Humphrey. This manuscript will likely be published in the 7th Proceedings of the Western States and Provinces Deer and Elk Workshop where it was presented.

Chapter IV is titled: “Observations on capturing and aging deer fawns.” Authors are Shawn P. Haskell, Warren B. Ballard, David A. Butler, Nicole M. Tatman, Mark C. Wallace, Christopher O. Kochanny, and O. Alcumbrac. This manuscript is scheduled for publication in December 2007 in the *Journal of Mammalogy*.

Chapter V is titled: “Factors affecting birth dates of sympatric deer in west-central Texas.” Authors are Shawn P. Haskell, Warren B. Ballard, David A. Butler, Mark C. Wallace, Thomas R. Stephenson, O. Alcumbrac, and Mary H. Humphrey. This manuscript is scheduled for publication in February 2008 in the *Journal of Mammalogy*.

Chapter VI is titled: “Productivity, mortality, and antipredator strategies of female and fawn deer in west-central Texas: a tale of 2 species.” Shawn P. Haskell will be first author, but co-authorship is undetermined at this time. This manuscript was drafted for *Wildlife Monographs* but has not yet been submitted.

CHAPTER II

ACCOUNTING FOR RADIOTELEMETRY SIGNAL FLUX IN TRIANGULATION POINT ESTIMATION

Abstract: Triangulation by radiotelemetry is a method commonly used to estimate locations of wildlife. Despite the importance of the accuracy of resulting location estimates, there has been little development and comparison of alternative methods for point-location estimation for 25 years. Most methods assume that signal transmissions as received are consistent, but signal heterogeneity and fluxing is common. Using data from a beacon study, we determined that a subjective ranking of confidence in the accuracy of a signal was correlated with absolute bearing error. Using this factor and the distance from a telemetry station to the error triangle incenter, we developed an algorithm to place a weighted point-location estimate in relative proximity to each error triangle leg. We have termed this the weighted-incenter method. Despite previous findings that the major confidence ellipse axis of Lenth's maximum likelihood estimator (MLE) correlated best to linear distance error, our beacon test data indicated that total bearing angle difference was the best single predictor of linear error with an optimal total angle of about 100°. The new and intuitive weighted-incenter method offered some improvement over previous methods such as the MLE estimator but only with suboptimal angle bearings that may be common in field studies. By using a MATLAB function to produce data for site specific regression analyses, one can determine which method should produce the more accurate point-location estimate for each triangulation observation. Further significance of this study for field biologists is discussed.

Key words: accuracy, maximum likelihood, methods, weighted-incenter

INTRODUCTION

Radiotelemetry continues to be a common method for obtaining wildlife location data (White and Garrott 1990, Millspaugh and Marzluff 2001). Once it is determined that field methods and equipment produce data of sufficient quantity and quality to accomplish study objectives, the next step is to use a standardized software package to obtain point-location estimates. Despite the importance of preliminary analyses of raw field data for subsequent hypothesis testing and inferential conclusions, there has been little direct comparison of software packages and techniques (Larson 2001), and few point-location estimation methods have been proposed since those of Lenth (1981) over 25 years ago.

Several potentially interacting factors such as operator and equipment error, topography, vegetative characteristics, animal movement, electromagnetic interference, and distance from transmitter to receiver can affect the accuracy and precision of radiotelemetry bearings and ultimately a point-location estimate (Withey et al. 2001). The most commonly used triangulation location estimators such as the maximum likelihood (MLE) and Andrew’s methods (Lenth 1981) generally assume homogeneous quality of received signals. Pace and Weeks (1990) produced a nonlinear weighted least-squares estimator by accounting for heterogeneous error variances associated with each telemetry station. This method requires labor intensive beacon testing at each station by considering variables such as distance, direction, and vegetative characteristics but demonstrated some improvement over previous estimators under certain conditions (Pace and Weeks 1990). Beacon studies are used to detect telemetry system biases, assess efficacy of confidence polygons, and create regression formulas to estimate linear distance errors which can direct the data censoring process. Beacon studies are therefore important for most projects using radiotelemetry, for effects appear to be site specific (White and Garrott 1990, Withey et al. 2001). However, a beacon study such as that required for the nonlinear weighted least-square estimator (Pace and Weeks 1990) may be labor intensive beyond the means of many field biologists, especially for those employing a mobile telemetry system with dozens or even hundreds of usable stations. Furthermore, while bias variability among small-scale time intervals at a given telemetry station due to factors such as electromagnetic interference is undetectable to the observer, signal flux caused by other factors such as long-wave radiation, topography, distance, and animal movement is detectable and can be subjectively quantified during each observation.

Using a truck-mounted null-peak radiotelemetry system at our study site, we recognized that all signals were not equally received. Some signals were strong with a distinct null, some had wide nulls, some faded in and out making it difficult to locate the null boundaries precisely, while others were so weak as to be detected reliably only with the peak. Therefore, we began recording a subjective measure of our confidence in the accuracy of each signal which we called "signal strength". Our objectives were to: 1) determine if the subjective measure of signal strength was correlated to absolute bearing error by conducting a beacon study, and if so, 2) create an intuitive point-location estimator by incorporating both signal strength and distance from a telemetry station to the incenter of the error triangle to assign relative weights to each of the 3 legs that define the error triangle, and 3) compare the performance of this estimator to others that are currently used.

STUDY AREA

We conducted the beacon study in west-central Texas where 66 radio-collared deer (*Odocoileus virginianus* and *O. hemionus*) were regularly relocated by triangulation. The study site was located on 4 contiguous private ranches comprising about 250 km^2, of which a central area of 88 km^2 contained the monitored deer. The area has been depicted as a transition zone between the Great Plains and Southwest Deserts ecoregions (Heffelfinger et al. 2003), and it was located where Texas' Edwards Plateau begins to descend into the Trans-Pecos desert. Elevations ranged from about 750 m ASL along a central riparian corridor to about 870 m ASL on mesa tops. Lowlands dominated by mesquite (*Prosopis glandulosa*), creosote (*Larrea tridentata*), tarbush (*Flourensis cernua*), and cactus (*Opuntia* spp.) and mesa slopes and tops dominated by juniper (*Juniperus* spp.) and yuccas (*Yucca* spp.) were nearly equally abundant within the study site. Riparian corridors supported thickets of hackberry trees (*Celtis occidentalis*) and relatively dense vegetation in general.

METHODS

In December 2004, we placed 9 radio-collars (6 Model M2610, Advanced Telemetry Systems Inc., Isanti, MN, USA, and 3 MOD-600, Telonics Inc., Mesa, AZ, USA) across the study site in localities and cover types typically used by deer of both species (Avey et al. 2003). Collars were placed from 0–1 m above ground to simulate bedding, feeding, and standing deer. We marked these locations with a WAAS-enabled Garmin GPS 76 global positioning system (GPS; Garmin International Inc., Olathe, Kans.) designed to provide accuracy to <3 m 95% of the time; when marking locations we allowed enough time for UTM eastings and northings to stabilize on the GPS unit while in “3D Differential” mode. We used a telescopic vehicle-mounted null-peak antenna system (Balkenbush and Hallett 1988) and 39 GPS-marked telemetry stations to conduct triangulations. We triangulated the 9 radio-collars 3 times each. We considered independence of triangulation observations on the same radio-collar achieved by varying the combination of telemetry stations used for that particular collar; triangulation geometry and other potential sources of error were always different for each of 3 triangulations conducted on a single collar. Telemetry stations were chosen to provide a combination of distances to transmitters and both total and interior bearing angles which simulated realistic conditions for telemetry data collection while also including unquantified topographic and electromagnetic interference. Triangulation bearings from the receiving antenna to transmitters were estimated with a hand-held Suunto® Navigator sighting compass (Suunto, Vantaa, Finland) declinated to true north; actual bearings were determined using the GPS coordinates. We sighted bearings from telemetry stations to GPS-marked landmarks visible on the landscape to assess potential compass-related bias. We examined system precision by taking duplicate bearings from a single telemetry station to a radio-collar after adjusting the compass >90° between iterations. Triangulation was most often performed from dirt ranch roads, but a paved road with adjacent power lines was used as well.

We used LOAS™ version 2.06 (Ecological Software Solutions, Urnäsch, Switzerland) to estimate transmitter point-locations, linear error distances, and confidence ellipses from the MLE, Andrew’s, Huber, and mean triangulation methods as well as the “Best Biangulation” method. We used MATLAB 6.5® (The MathWorks, Inc., Natick, Mass.) to construct a function capable of accepting raw radiotelemetry data and outputting data potentially correlated with linear distance errors (e.g., distances, angles, and error triangle parameters), realized bearing and linear distance errors to known transmitter locations, and a new weighted-incenter point-location estimate. The weighted-incenter estimator is an algorithm that begins by placing a point at the incenter of the error triangle generated by 3 rays originating from the 3 telemetry stations used for a single triangulation observation; a closed triangle is not required. The incenter is a point within a triangle that is equidistant to the 3 defining legs which would be equivalent to the centroid of an equilateral triangle; it is also the point of intersection among the 3 interior angle bisectors. Each leg of the triangle was given a relative weight determined by 2 factors associated with the corresponding bearings recorded at each telemetry station; these were: 1) distance from the station to the incenter, as linear error caused by bearing error becomes magnified with distance (Saltz and Alkon 1985), and 2) a subjective confidence ranking of the bearing based on the strength of the received signal (Table I). Weighting was accomplished by relative ratios. A relative ratio for distance was determined by dividing the shortest distance by each of the 3 distances associated with a single triangulation observation so that the shortest distance was given a ratio equal to 1. A relative ratio for signal strength was determined by dividing each signal strength value by the highest of the 3 so that the highest value was given a ratio equal to 1. The 2 ratios associated with each bearing were multiplied to give a combined weight. The highest ratio among the 3 bearings for each triangulation observation was divided by the middle and lowest ratios, and the middle ratio was divided by the lowest to determine final relative weights for each leg of the triangle. For example, for 3 bearings (A, B, and C) taken from telemetry stations that are 150 m, 250 m, and 500 m from the error triangle incenter with signal strength rankings of 3, 3.5, and 3, respectively, it is determined that distance ratios are equal to 1, 0.6, and 0.3, and signal strength ratios are equal to 0.86, 1, and 0.86, respectively. Combined ratios are equal to 0.86, 0.6, and 0.26, respectively. By dividing these as described above it is determined that the point-location estimate should be 1.43 times closer to leg A than leg B, 3.31 times closer to leg A than leg C, and 2.31 times closer to leg B than leg C. The algorithm then proceeds by determining if the current point-location satisfies these 3 criteria within 3 m; if so, the point-location estimate is finalized; if not, the program moves the point either towards or away from leg of interest, recalculates distances, and continues to check criteria until satisfied.

We used S-PLUS® 6.2 for Windows (Insightful Corp., Seattle, Wash.) to perform stepwise regression analyses to generate predictive models for estimating linear distance errors for each point-location estimation method and the differences in linear errors between the MLE and weighted-incenter methods (i.e., which method should perform better for a given triangulation observation). We used Microsoft® Office Excel 2003 (Microsoft Corp., Redmond, Wash.) to initially examine simple scatter plot correlations. Variables initially considered included total and interior acute and obtuse bearing angles, mean signal strength, area of the error triangle, mean, shortest, and longest lengths of error triangle legs, major error ellipse axis length and ellipse area (MLE only), mean, shortest, and longest distances from telemetry stations to predicted locations (or distance to the common incenter for comparison of MLE and weighted-incenter methods), and distance from the telemetry station centroid to the predicted location; quadratic expressions were used when evident in simple correlations. Only those variables that appeared to have substantial explanatory effect (r^2>0.10) were entered into final stepwise procedures to reduce the potential for spurious results caused by an overabundance of variables; some competing intercorrelated variables were kept to allow for comparative interaction with non-correlated variables (Neter et al. 1996). We checked predictive accuracy of competing models against true errors and presented the ones that performed best.

RESULTS

We estimated locations of 9 radio-collars via triangulation 3 times each for a total of 27 triangulation observations and 81 recorded bearings. Although quite variable, absolute bearing error was negatively correlated with signal strength giving impetus for the development of a new point-location estimator incorporating the subjective confidence ranking of each bearing estimate (Figure I). The mean of the 81 signed bearing errors indicated a 4° positive bias. Mean linear distance error using the MLE estimator decreased from 190.6 m to 112.8 m after correcting for this bias (Table II). Compass readings to visible landmarks indicated that the bias was inherent to the radio-tracking system and not the compass. Fortuitously, about 3 months after conducting the beacon study we were able to confirm the 4° system bias visually by taking compass bearings and null antenna readings on a radio-collared deer in a clearing about 500 m from the vehicle. After correcting for the bearing bias, mean absolute bearing error was 2.3° (±0.5° 2SE). Precision of the radio-tracking system was excellent; the mean difference of 11 cases when duplicate bearings were taken from a telemetry station to a transmitter was 0.7° (range = 0–2°). By chance, the greatest linear distance error of 438 m was associated with the smallest error triangle having an area of 3.0 m^2 and shortest leg length of 2.0 m. This outlier was not used in regression analyses to determine factors associated with linear error for a particular point estimation method, for it has previously been found that the length of the major error ellipse axis for the MLE estimator, which was highly correlated with the length of the shortest error triangle leg ($r^2 = 0.943$), was the best predictor of linear distance error (Saltz and White 1990). We suggest that while random aberrations such as this occur in telemetry studies, they are unpredictable and can not be identified from field data.

The 3 point-location estimation methods proposed by Lenth (1981) performed nearly equally with the beacon study data (Table II). The "Best Biangulation" method available in LOAS performed worse on average than other methods but primarily due to observation #14 (Table II); without this observation the mean linear distance error would have been 129.0 m. Observation #14 contained the most acute interior angle of 4° resulting in the most acute and elongated error triangle; the biangulation procedure chose an estimated location at the vertex farthest from the transmitter location. Similarly, the mean methods performed poorly with acute interior angles, as they simply estimated a location at the centroid of the elongated error triangle. The new weighted-incenter method performed similar to Lenth's (1981) estimators but on average estimated point-locations 3.9 m farther from the transmitter locations (Table II). The difference between performance of the weighted-incenter and MLE methods was best explained by quadratic relationships of total bearing angle, length of the shortest error triangle leg, and acute interior angle, in order of individual significance. As the total bearing and acute interior angles deviated from about 95° and 35°, respectively, the weighted-incenter method performed better, but as the shortest error triangle leg extended beyond about 100 m, the MLE method performed better (Figure II). A multiple regression equation incorporating these 3 factors explained 68% of the error variance ($P \leq 0.001$).

The single factor best explaining linear distance error for the MLE estimator was total bearing angle difference. As the total bearing angle deviated from about 100°, linear distance error increased (Figure III). The other 2 factors that added significance to the selected regression model explaining linear error were a positive correlation with the length of the shortest error triangle leg and a negative correlation with mean signal strength, in order of significance. A multiple regression equation incorporating these 3 factors explained 80% of the error variance ($P \leq 0.001$). The same 3 factors in identical order of significance were also selected in a regression model explaining linear error for the weighted-incenter method. However, the significance level of each factor was less, but the model still explained 74% of the error variance ($P \leq 0.001$).

DISCUSSION

Results from our beacon study and development of the weighted-incenter method are important in 2 ways. First, our results reiterate the conclusions of previous investigators (e.g., White and Garrott 1990, Withey et al. 2001) that beacon studies are necessary for most projects relying on radiotelemetry triangulation data to test spatial hypotheses; exceptions may include rare cases where realized inaccuracies are insignificant to the hypotheses being tested. Recognition and quantification of a 4° bearing bias in our tracking system could only have been determined with a beacon study. It has been suggested that it may be better to ignore systematic direction bias when locating the source of a signal (Lenth 1981), but correction for our system bias reduced linear distance errors significantly. Regression parameters explaining linear errors will likely vary among study sites and field methods used. These regression equations can best predict error associated with each triangulation observation which can subsequently be used to assess the power of analyses at various spatial scales (Withey et al. 2001, Findholt et al. 2002). Using a truck-mounted tracking system, some researchers found that deviation from a total bearing angle of 90° and distance from receiver to estimated location explained 82% of the variance in linear error (Wallingford and Lancia 1991). Others did not consider bearing angles irrespective of distance in computer simulations and found that the length of the major axis of the MLE error ellipse was the best predictor of linear error (Saltz and White 1990). Our results concurred with those of Wallingford and Lancia (1991) that total bearing angle was the best predictor of linear error, but similar to other studies (Hupp and Ratti 1983, Kufeld et al. 1987), we did not find distance from receiver location to predicted transmitter location to be a major influence despite a mean distance of about 1,500 m (range = 414–3,231 m). Our results indirectly concurred with those of Saltz and White (1990) in that the length of the shortest error triangle leg, which was highly correlated with the length of the MLE major ellipse axis, was also a significant determinant of linear error. Interestingly, the mean of the subjective signal confidence rankings for each triangulation observation also added explanatory power to both the MLE and weighted-incenter methods.

Another contribution of this study was the testing of often used estimation methods against a new intuitive method accounting for heterogeneity among received signals. Previous methods such as the MLE, Andrew's, and Huber estimators performed similarly and overall outperformed the new weighted-incenter method by an average of about 4 m. However, this new method appears to offer improvement to previous methods when angle bearings, both acute interior and total, are suboptimal while the shortest error triangle leg is not longer than about 100 m (Figure II).

Suboptimal triangulation angles are undesirable but may be unavoidable. While it appears evident that to minimize inaccuracies field biologists should strive to achieve 90–100° of total bearing separation within a triangulation observation, this may not always be possible given access, topographic, or time limitations. A mobile field biologist may use a map or handheld GPS unit to locate a 3rd telemetry station that should produce optimal total bearing separation after the 1st 2 bearings are recorded; the acuteness of the 1st angle appears less important. With this information in mind, we collected 66 triangulation observations in 2 days; total bearing angles were often suboptimal with 36 either <65° or >125° in the ranges where the weighted-incenter method may be most desirable (Figure IV). For final point-location estimation with the MATLAB function as a means to output necessary data, we can use the regression model explaining the difference in linear distance errors between the weighted-incenter and MLE methods to predict which estimator would likely generate the more accurate point-location for each triangulation observation and then use the appropriate estimator to maximize accuracy for each observation. Estimations of location inaccuracies can be made with a second regression model; these can be used to censor location data according to research objectives and hypotheses being tested. While our sample size of 27 triangulations would be close to the minimum desired for a beacon study, model fits were high. A greater sample size, perhaps near 50, would probably be preferable to increase predictive power if necessary for accuracy required by research objectives. The true optimal total bearing angle may or may not lie closer to the 90° value reported by Wallingford and Lancia (1991); it is possible that the relative paucity of total bearing angles greater than this value sampled during this beacon study affected the relationship (Figure III).

The weighted-incenter method we presented may have further drawbacks and benefits. The bearing confidence ranks on which it relies were subjective and may be difficult to standardize among observers. However, the most important consideration for the confidence rank is that it is relatively consistent within each triangulation observation; as long as the 3 signals are ranked accurately respective of one another, the estimator should operate as intended. The MATLAB function as programmed only accepts 3 bearings for each triangulation observation. Other methods such as the MLE are currently more appropriate for radiotelemetry point estimation with other than 3 bearings (i.e., not triangulation). We observed little variability in signal strength during our beacon test study (Figure I) though greater variability may be more common in field studies (Figure V). We did not fix radio-collars around plastic bottles filled with saline to reduce signal strength as has been recommended for beacon studies (Hupp and Ratti 1983). It is logical that the weighted-incenter method should perform as well or better relative to other methods when signal strength ranks are more variable, but further beacon testing should incorporate methods to produce signals from radio-collars that are weaker than those we received. The signals we received were often too strong to rank signal strength as "4" because a silent and distinct null was unattainable. This new method may facilitate data entry by allowing each triangulation observation to be entered into a single row within a software spreadsheet thereby reducing repetitive typing of grouping variables. MATLAB is an excellent tool for techniques such as those described in this paper because the programmer can obtain most any information deemed useful. For example, if a triangulation observation produces rays that do not intersect because the radio-transmittered animal is close to a telemetry station or 1 or more bearings are deviant, the generated output can inform the programmer to examine the observation with a figure plot. We have programmed MATLAB to produce such a plot, but the MapSource™ software (Garmin International Inc., Olathe, Kans.) designed to store GPS data over a topographic layout can also be used in such a way and can help a researcher become familiarized with telemetry stations at a study site.

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Table 2.1. Criteria for determining subjective confidence ranks (i.e., signal strength) for a signal received during radiotelemetry triangulation procedures using a null-peak system to be used in the weighted-incenter point-location estimator.

Signal strength	Criteria
4	Signal loud and steady; null very distinct (<1° wide)
3.5	Signal loud and steady; null distinct (<2° wide)
3	Softer signal but mostly steady; null less distinct (<5° wide)
2.5	Some signal flux; null edges less clear (<10° wide)
2	Signal flux prevalent; null edges fade in and out (<20° wide)
1.5	Signal faint and fluxing; peak may be used as well as null (<30° wide)
1	Signal heard on peak only; bearing error maybe >15°; do not use

Table 2.2. Linear distance errors (m) for triangulation observations using the Andrew's, Huber, mean, maximum likelihood (MLE), and weighted-incenter (WI) methods as well as the "Best Biangulation" (BB) procedure in LOAS. Differences between WI and MLE methods are presented. Each 3 consecutive observations are from the same radio-collar.

	Linear distance errors (m)						
Obs. #	Andrew's	Huber	Mean	BB	WI	MLE	WI–MLE
1	42.3	41.6	25.1	28.7	35.1	41.6	-6.5
2	36.2	35.6	22.4	29.7	27.1	35.6	-8.5
3	44.3	42.5	26.2	69.8	33.0	42.5	-9.5
4	93.1	93.3	90.8	73.0	92.1	93.3	-1.2
5	154.0	157.7	371.9	73.1	138.9	157.7	-18.7
6	59.8	59.6	95.9	24.1	64.6	59.6	5.0
7	82.0	82.0	81.4	82.7	81.7	82.0	-0.2
8	151.7	148.5	130.5	62.8	119.1	148.5	-29.4
9	149.2	150.0	163.4	165.3	158.9	150.0	8.9
10	364.7	365.6	278.5	304.6	341.8	365.6	-23.8
11	437.9	437.9	437.2	437.4	437.6	437.9	-0.3
12	29.3	29.9	54.5	39.3	39.1	30.0	9.1
13	165.0	165.2	164.8	175.9	165.1	165.2	-0.1
14	121.3	117.3	699.3	2062.2	110.4	117.3	-6.9
15	97.2	96.8	86.2	87.5	93.8	96.8	-3.0
16	38.8	44.7	156.5	158.0	65.0	44.7	20.3

Table 2.2. continued

17	30.3	30.2	29.5	44.9	30.8	30.2	0.6
18	34.7	33.4	34.0	82.4	30.6	33.4	-2.8
19	93.6	98.8	443.6	25.9	165.0	98.8	66.2
20	261.0	261.4	285.1	304.4	282.2	261.4	20.9
21	98.2	98.5	87.0	87.3	96.4	98.5	-2.1
22	46.9	47.3	54.2	22.1	52.9	47.3	5.6
23	17.7	18.7	47.7	116.5	29.1	18.7	10.5
24	22.3	22.0	23.3	35.8	21.8	22.0	-0.1
25	149.6	152.1	248.9	513.7	198.9	152.1	46.8
26	104.1	107.5	137.5	223.9	113.4	107.5	5.9
27	104.5	108.1	185.5	85.2	126.3	108.7	17.6
Mean	112.2	112.8	165.2	200.6	116.7	112.8	3.9
2SE	39.0	39.0	63.1	151.3	38.9	39.0	7.5

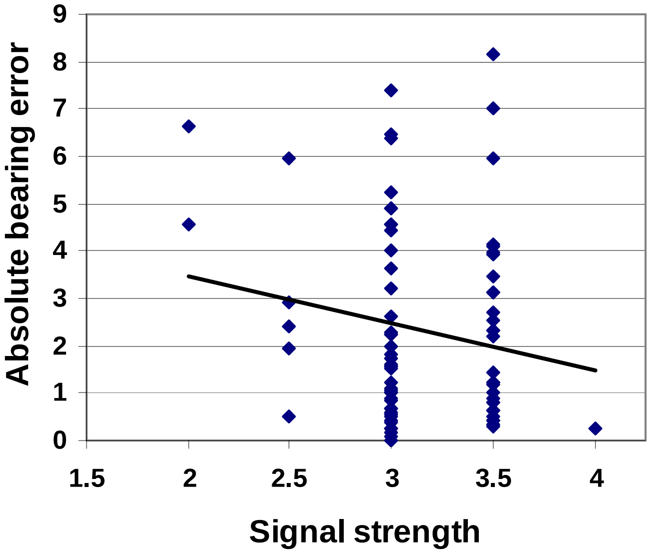

Figure 2.1. Absolute bearing error (degrees) versus subjective bearing confidence (i.e., signal strength) recorded during a radiotelemetry beacon study in west-central Texas, December 2004. Trendline is linear least-squares regression.

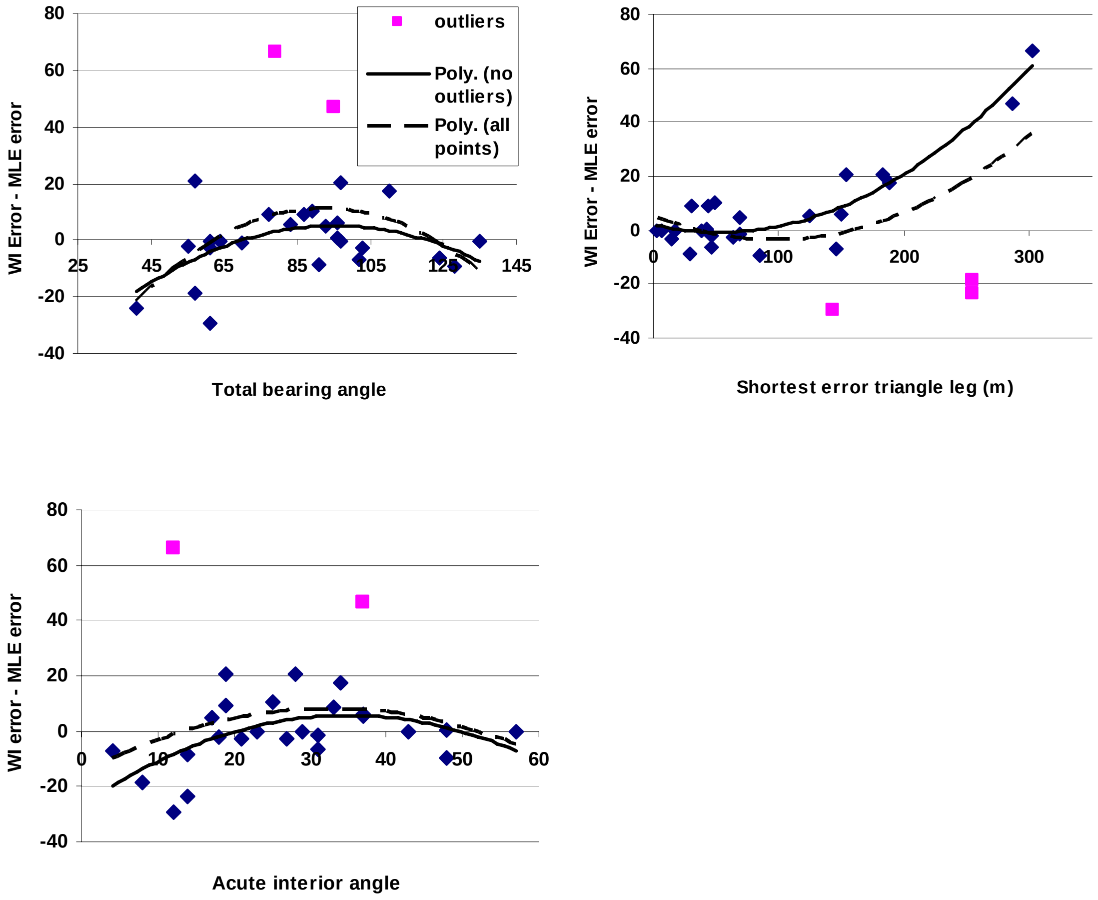

Figure 2.2. Factors best explaining the differences in linear distance errors between the weighted-incenter and MLE triangulation point-location estimators in order of individual significance: total bearing angle (degrees; top), length of the shortest error triangle leg (m; middle), and acute interior angle (degrees; bottom). Quadratic trendlines are shown with and without outliers to illustrate a range of relationships as alternate factors within the regression model explain additional variation.

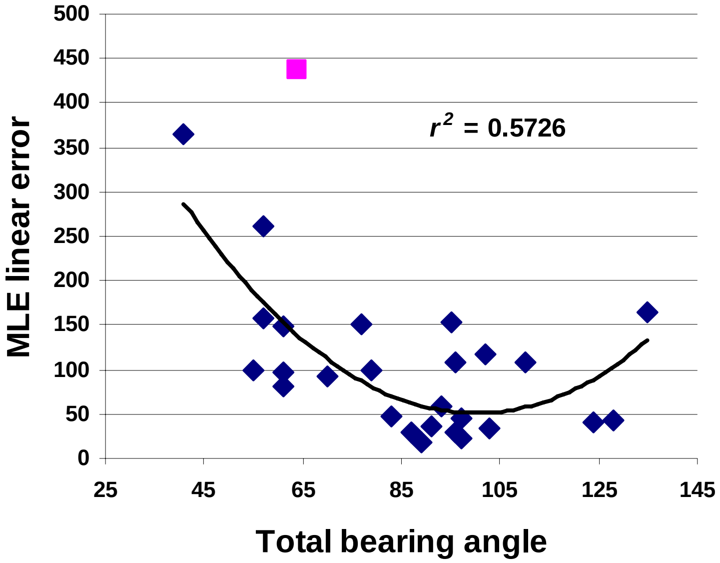

Figure 2.3. Total bearing angle (degrees) versus linear distance errors of the MLE triangulation point-location estimator. The square outlier not used in individual regression analyses explaining linear error for the MLE or weighted-incenter methods.

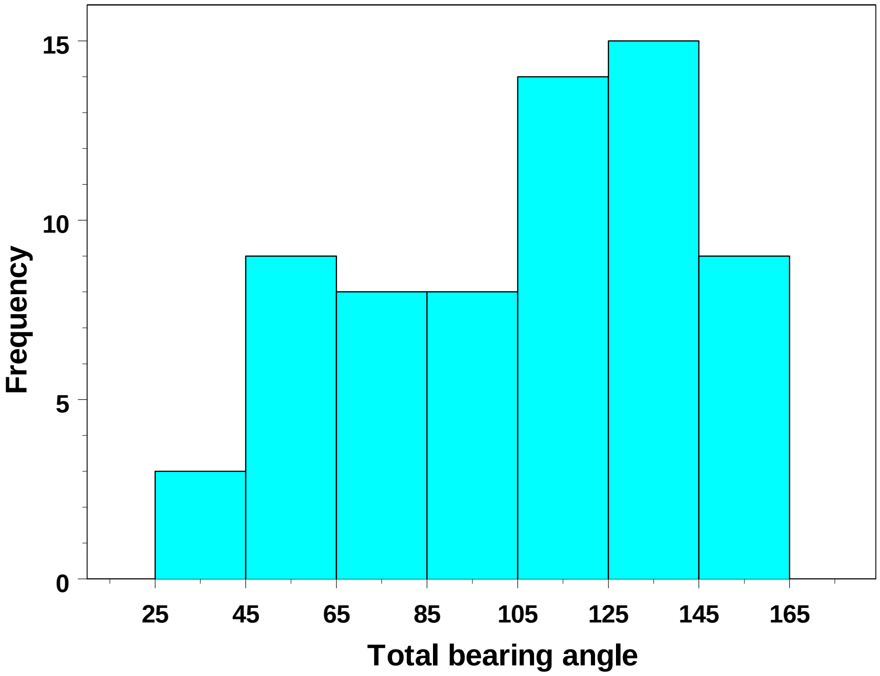

Figure 2.4. Frequency distribution of total bearing angles from triangulation observations obtained while radio-tracking 66 deer in west-central Texas, February 2005.

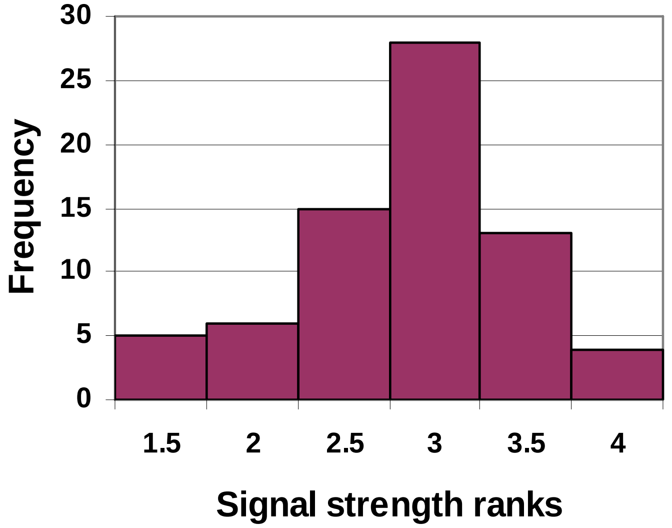

Figure 2.5. Frequency distribution of 71 signal strength ranks collected during triangulation of radio-collared deer in west-central Texas, May 2005.

CHAPTER III

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

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, distance sampling, roads, spotlight, thermal infrared

INTRODUCTION

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, Msoffe et al. 2007, Wiewel 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, etc.); in such cases, comparisons among methods are only relative and true accuracy or bias cannot be examined (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 and data are collected during environmental conditions that promote deer movement (Haskell et al. 2006). 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 km^2) 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 pinchotii*) communities with sparse varying herbaceous vegetation. Slopes and rim-rock 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), a radiocollar (Telonics, Mesa, Arizona, USA and ATS, Isanti, Minnesota, USA), and a numbered ear-tag. The VITs were used to help locate neonates for capture (Haskell et al. 2007). When neonates were found they were fitted 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 periods (i.e., days). 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 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 km^2). 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 radiotelemtry 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 km^2 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 km^2 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/km^2 (Fig. 3).

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/km^2, SE = 4.3, range

= 6.1–42.6 deer/km^2). 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, Fig. 3). 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).

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/km^2 rather than 29 deer/km^2 and very near the distance sampling point estimate of 31 deer/km^2 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 a. 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).

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).

CONCLUSIONS

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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Table 3.1. 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 km^2), 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.

Method	Key model	Series expansion	K	$Pr>\chi^2$	ΔAIC	Deer density	CV	ESW	CV	Cluster density	CV
SL	HR	NA	2	0.125	0.00	31.0	0.242	99.18	0.09	0.149	0.221
	U	CO(2)	2	0.056	1.25	35.0	0.240	87.74	0.08	0.168	0.219
	HN	NA	1	0.070	3.96	33.2	0.235	92.23	0.07	0.160	0.213
TIR	HR	NA	2	0.328	0.00	35.0	0.239	97.12	0.10	0.152	0.215
	HN	NA	1	0.253	0.80	37.6	0.233	90.29	0.08	0.163	0.208
	U	CO(2)	2	0.196	1.69	38.3	0.236	88.72	0.09	0.166	0.212
Combined	HR	NA	2	0.107	0.00	37.5	0.229	100.14	0.09	0.173	0.208
	U	CO(2)	2	0.022	2.38	42.3	0.223	88.75	0.07	0.195	0.200
	HN	NA	1	0.026	3.43	39.9	0.223	94.06	0.07	0.184	0.200

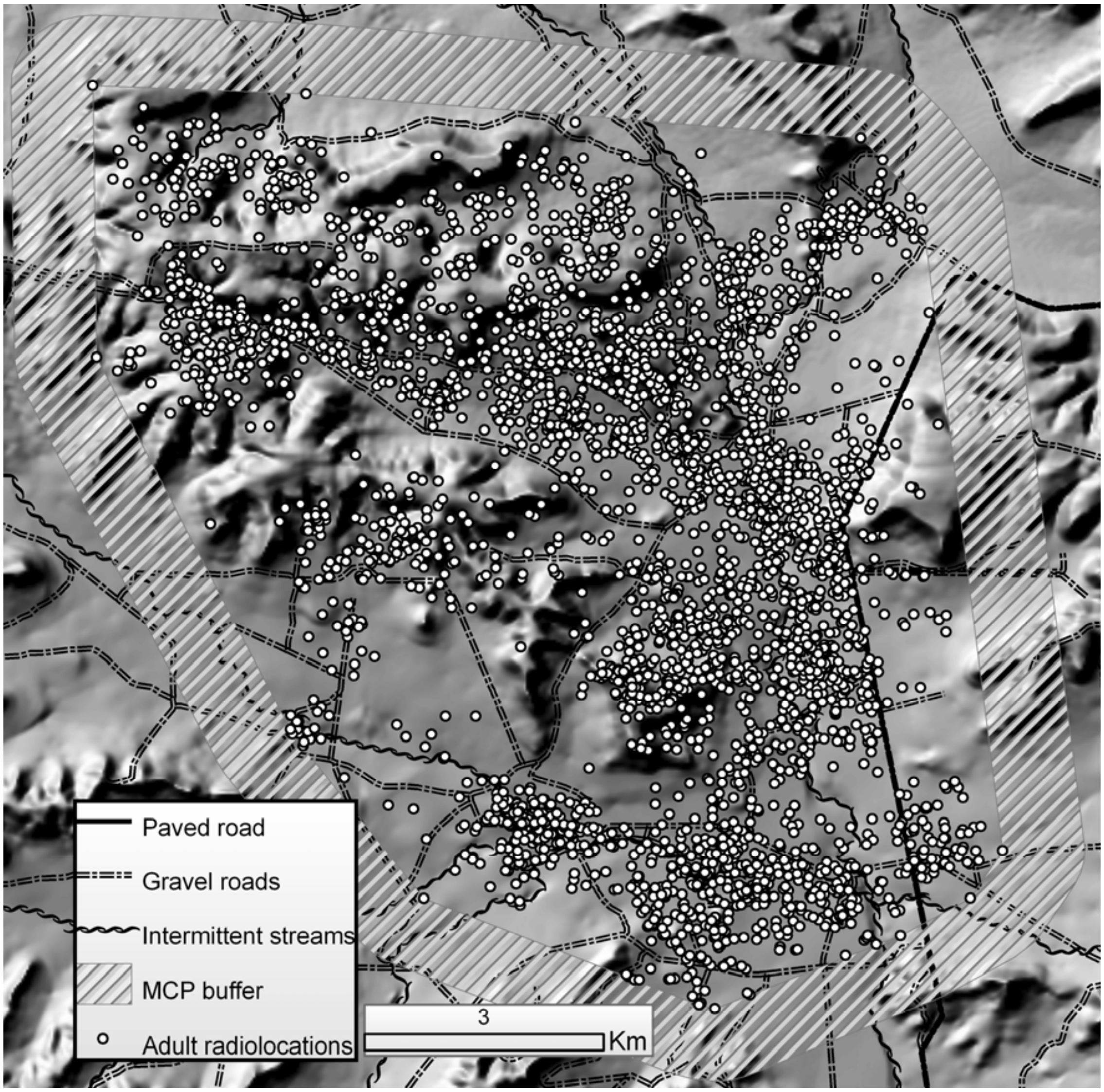

Figure 3.1. Study site for 2004–2005 deer surveys in northwest Crocket County, Texas, showing topography, individual deer locations, and minimum convex polygon (MCP) of all locations with 884-m buffer as effective sample area estimates. Main secondary caliche road surveyed leaves paved road near northeast 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).

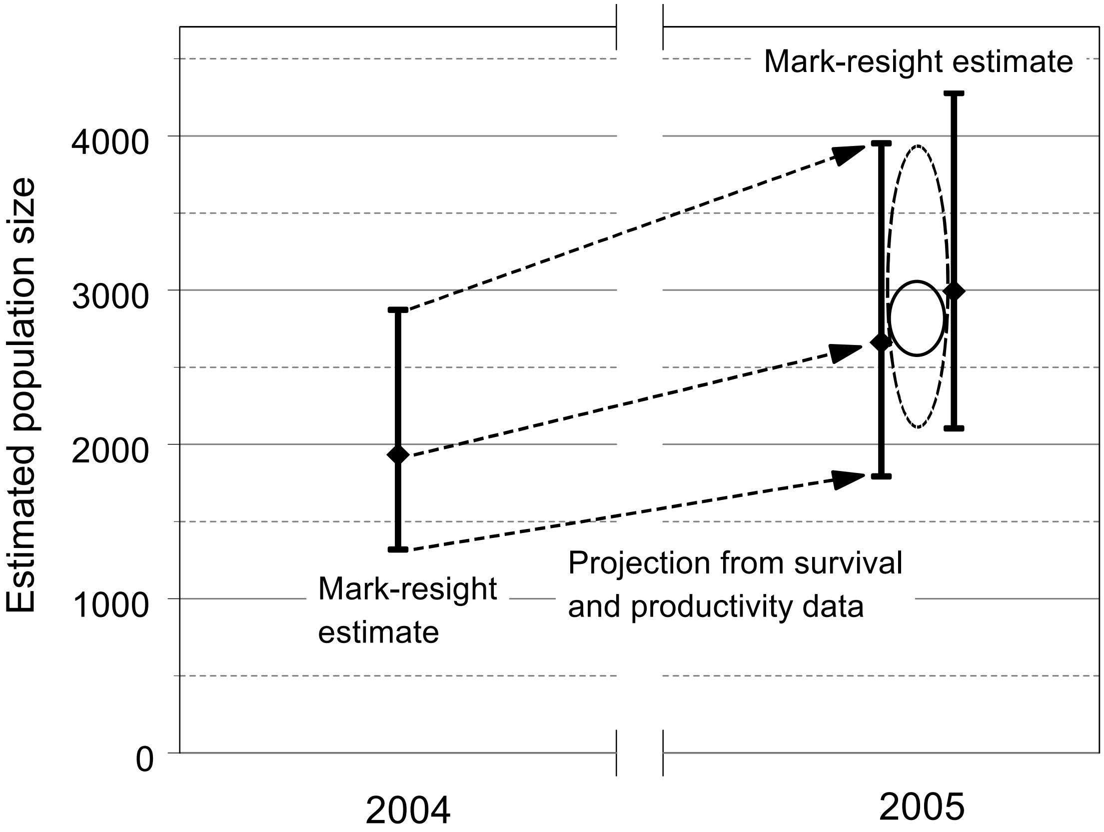

Figure 3.2. Mark-resight population estimates from winter deer surveys in northwest Crockett County, Texas, 2004 and 2005. Estimate from 2004 projected into 2005 based on unpublished demographic vital rate data for a priori prediction and post hoc refinement of 2005 estimate. Larger ellipse illustrates combined 95% confidence intervals, and smaller ellipse illustrates subjective determination of a reliable estimated range of 2600–3050 deer in 2005.

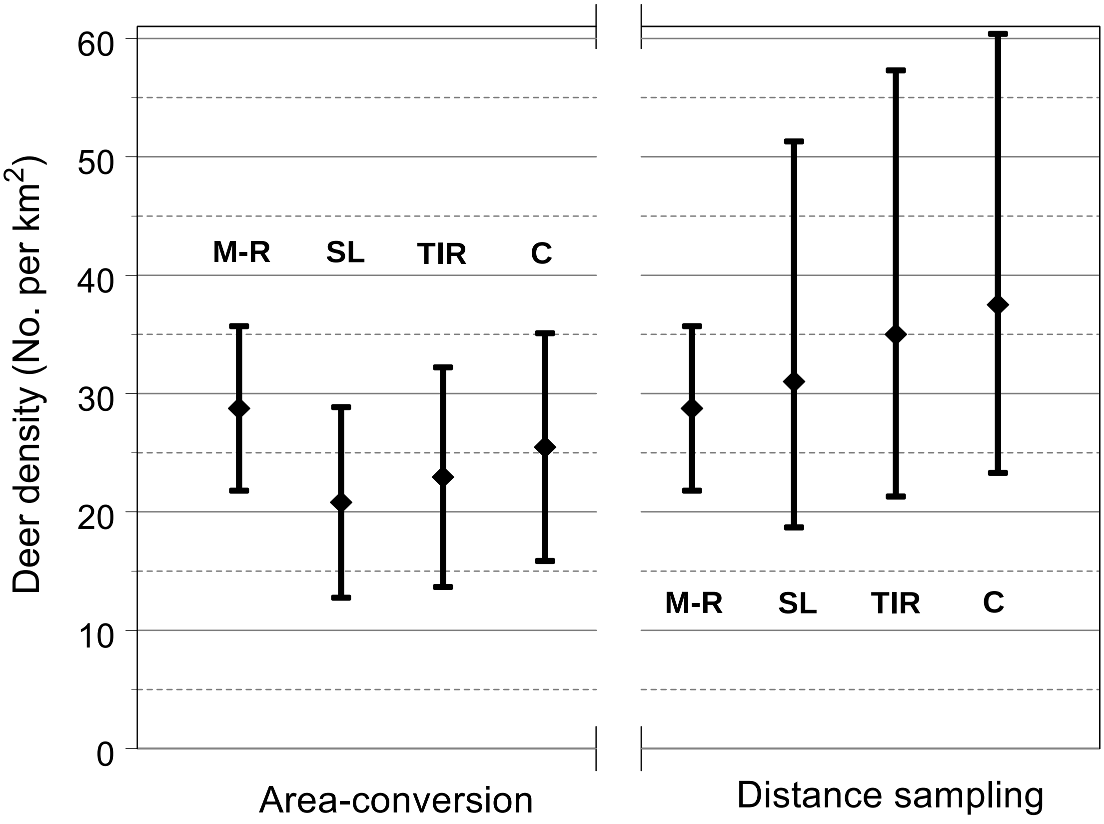

Figure 3.3. Deer density estimates by nighttime surveys in northwest Crockett County, Texas, during November 2005 with a mark-resight (M-R) estimate as an independent comparative baseline. Estimates are from area-conversion (assuming 100% detectability) and distance sampling techniques using spotlighting (SL), thermal infrared imaging (TIR), and combined (C) methods. Error bars are 95% CIs around expected means.

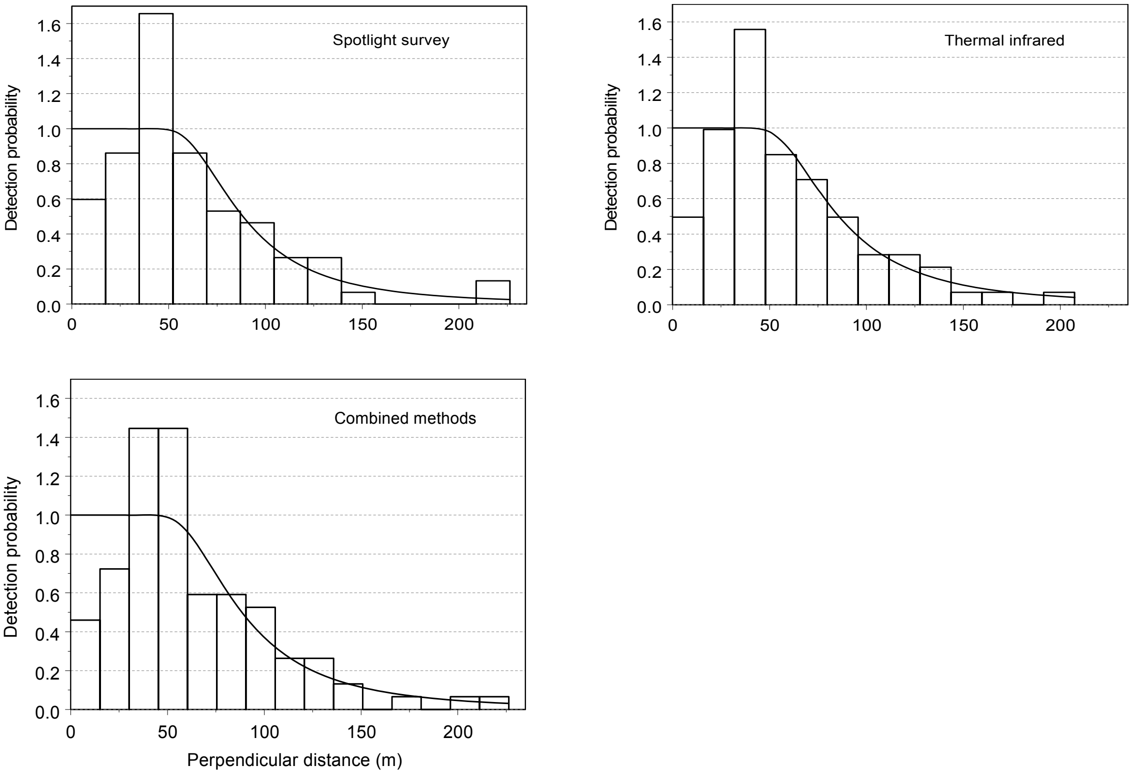

Figure 3.4. Detection probabilities versus distance from roads resulting from preferred hazard-rate distance sampling models of nighttime deer survey data from northwest Crockett County, Texas, in November 2005 by spotlighting (SL), thermal infrared imaging (TIR), and combined methods. Histogram bins 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 15.1m for combined as default output data from the program Distance.

CHAPTER IV

OBSERVATIONS ON CAPTURING AND AGING DEER FAWNS

Abstract: During a fawn mortality study of sympatric white-tailed (*Odocoileus virginianus*) and mule deer (*O. hemionus eremicus*) in west-central Texas from 2004–2006, we made observations that should help deer researchers increase their efficiency of fawn capture, obtain better estimates of fawn ages, and obtain more reliable fawn survival estimates. We experimented with vaginal implant transmitter (VIT) designs and found that larger holding wings and antennas protruding < 1 cm past the vulva resulted in more successful drops at birth-sites. White-tailed fawns moved farther from birth-sites than mule deer fawns of similar ages ($P = 0.027$). Our model predicted that white-tailed and mule deer fawns moved an average of 100 m away from birth-sites after 12.5 and 17.5 h postpartum, respectively; outliers may be expected. Compared to previously published models estimating captive fawn ages from new hoof growth, our model predicted that free-ranging fawns were generally 1.5 weeks older. As others have suggested, marking induced abandonment was rare, and we suggest doe monitoring and fawn capture methods that could minimize such occurrences. Behavioral and morphological models as we describe may be species-, site-, and time-specific, and biologists should use caution when extrapolating inferences from captive animal-derived models to free-ranging populations.

Key words**:** aging, birth-sites, capture, fawns, mule deer, new hoof growth, *Odocoileus* spp, Texas, vaginal implant transmitters, white-tailed deer

INTRODUCTION

Population dynamics of large herbivores are generally influenced by juvenile survival and recruitment more than other demographic parameters in response to various intrinsic and extrinsic processes (Gaillard et al. 2000, Garrott et al. 2003). New technologies increase our capacity to define and understand reproductive biology and subsequent recruitment patterns. Methods used to estimate gross reproductive rates (Huang et al. 2000, Stephenson et al. 1995, Andelt et al. 2004), capture true neonates free of potential early-survivor bias (Garrott and Bartmann 1984, Carstensen et al. 2003, Bishop et al. 2007), and monitor subsequent survival (Steigers and Flinders 1980, Diefenbach et al. 2003) have been continuously updated. However, even if a deer (*Odocoileus* spp.) birth-site is located, fawn capture is not certain (Bowman and Jacobson 1998, Johnstone-Yellin et al. 2006). Deer researchers (e.g., Nelson and Woolf 1985, Ballard et al. 1999, Pojar and Bowden 2004, Carstensen Powell and DelGiudice 2005, Burroughs et al. 2006) have also attempted to capture random fawns of unknown age and rely on published morphometric models to predict fawn age; these models were generated from captive white-tailed (*O. virginianus*; Haugen and Speake 1958, Sams et al. 1996) and Rocky Mountain mule deer fawns (*O. hemionus hemionus*; Robinette et al. 1973).

During a research project investigating fawn survival of sympatric white-tailed and desert mule deer (*O. h. eremicus*) in west-central Texas, we made observations that other field researchers may find useful. These observations regard: 1) preferred vaginal implant transmitter (VIT) design for medium-sized free-ranging deer, 2) estimates of fawn movements from birth-sites as a function of time from birth to capture, and 3) estimates of age predicted by new hoof growth of free-ranging fawns. All three of these parameters should improve fawn capture success and improve age and survival estimates.

STUDY AREA

Our study site was located in west-central Texas, where the southwestern edge of the Edwards Plateau descends into the Trans-Pecos region. Heffelfinger et al. (2003) depicted this area as a transition zone between the Great Plains and Southwest Deserts ecoregions. Elevations ranged from 750 m ASL along a central riparian corridor to 870 m ASL on mesa tops. The area was primarily a shrub-dominated community without tall canopy cover except in riparian areas. During June–August, long-time average low and high temperatures at nearby Midland airport were 20°C and 34°C, respectively (National Oceanic and Atmospheric Administration 2006). Other researchers have described the area in greater detail (Avey et al. 2003, Butler et al. 2006).

METHODS

Field data

In late April 2004–2006, we captured 25 pregnant females of each deer species by net-gun from helicopter (Krausman et al. 1985), confirmed pregnancy status and estimated body fat content by ultrasonography (Smith and Lindzey 1982, Stephenson et al. 2002), and fitted pregnant does with very high frequency radiocollars (Telonics, Mesa, Arizona, USA; Advanced Telemetry Systems [ATS], Inc., Isanti, Minnesota, USA) and VITs (ATS, Inc.; Bishop et al. 2007). In 2004, VIT retention to parturition was less than expected based on a previous published account (Carstensen et al. 2003), so we consulted with the manufacturer to make the internal holding wings wider for 2005 and 2006. In 2006, the VIT antenna lengths were longer than the previous 2 years based on recommendations from a behavioral study of captive deer (Johnstone-Yellin 2006). However, from our previous experience we were concerned about deer orally removing their VITs before parturition. Therefore, we cut antennas that protruded greater than 2 cm past the vulva to < 1 cm, leaving some 1–2 cm, and applied super-glue to the cut ends to prevent fraying. For contingency table analyses examining effects of wing length (2004 versus 2005) and antenna length (within 2006) on successful VIT drops, we considered a “successful” drop as one that occurred within 30 m of a birth-site because to us that seemed a reasonable distance to enable detection of a fresh birth-site in this semi-arid brushy environment.

Vaginal-implant transmitters were programmed with: 1) a temperature-sensitive switch at 35°C to be triggered on expulsion, 2) a precise-event code (PET) to allow remote backdating of the switch to within 15 minutes, and 3) an active transmitting period of 12–14 h per day to preserve battery life, which often precluded precise backdating. Also, direct sunlight on a VIT at temperatures as low as 26°C could induce a false-negative “internal” signal (S. Haskell, personal observation). We monitored VIT signals from pregnant does daily between midnight and 0800 hours to avoid false-negative signals. Therefore, we relied not only on PET codes but also on evidence from birth-sites (e.g., freshness of sign and shade aspect relative to previous environmental conditions) and the last time the VIT was heard to approximate timing of a birth event. Many of these estimates were intervals such as 20–28, 12–24, or 8–14 h prior to fawn capture, but those < 8 h were precise to within 15 minutes by PET code, because we set VITs to begin transmitting at 2230 hours and usually began fawn searches at daylight around 0700 hours. We used the mean of these intervals as an independent variable for regression analysis predicting distance of fawn movements from birth-sites. In concordance with other observations (Johnstone-Yellin et al. 2006), we noted that some does expelled VITs early in labor, perhaps 1 or 2 h before parturition, so we allowed for these occurrences in our estimates.

When VITs were expelled, we first triangulated the VIT and doe by radiotelemetry (Haskell and Ballard 2007) and then initiated searches at sunrise after locating the doe by homing. We used handheld Global Positioning System (Model GPS 76; Garmin Inc., Olathe, Kansas, USA) to mark doe locations and birth-sites, track fawn-search grids directed towards the doe's location (M. Carstensen Powell, University of Minnesota, personal communication), and mark locations of captured fawns. To account for dependence of observations associated with twin captures, we calculated a single distance response from birth-site to capture location as the average of the 2 Euclidian estimates. Twins were determined by direct observation at capture and subsequent monitoring by radiotelemetry. We fitted each fawn with an expandable radiocollar (Diefenbach et al. 2003) and measured new hoof growth to the nearest 0.5 mm (Sams et al. 1996). With PETs on fawn radiocollars and daily monitoring practices, fawns ages at death were known to the level of precision of fawn ages at capture. Thus, we measured hoof growth from dead fawns (e.g., sickness and predation) to assess growth over a period of nearly 2 months.

Data analysis

We compared proportions using likelihood-ratio chi-square tests (Zar 1999). For regression analysis to estimate a function describing *distance* (m) fawns moved from birth-sites, we log-transformed the response variable and predictor variable of *age* (hours) to control influence of outliers and help satisfy the assumption of homoscedasticity (Neter et al. 1996, Zar 1999); we also investigated a potentially modifying *species* effect. To be consistent with previous models, we used linear least squares regression to predict fawn *age* (days) from *new hoof growth* (mm); again, we considered a potentially modifying *species* effect. However, to account for heterogeneous errors and predominance of potentially intercept-biasing zero hoof growth measures at neonatal capture, we used an inverse square-root function of *new hoof growth* for weighted least squares (Carroll and Ruppert 1988). We qualitatively compared our hoof growth model to 3 previously published models from captive fawns. We used SAS® 9.1 (SAS Institute Inc., Cary, North Carolina, USA) for statistical analyses and S-Plus® 7.0 (Insightful Corp., Seattle, Washington, USA) for data plots. All field operations complied with Texas Tech University Animal Care and Use Committee permit # 03075-10, which conformed to Animal Care and Use Committee (1998).

RESULTS

After adult mortalities (2 in both 2005 and 2006) and apparent VIT malfunctions were censored, we obtained data from 44, 46, and 44 VITs known to be functional when expelled in 2004, 2005, and 2006, respectively. In 2004, VIT wing length was shorter than in 2005 (5.90 cm versus 6.75 cm). We classified 30% (13 of 44) of VIT drops as successful in 2004 compared to 70% (32 of 46) as successful drops in 2005 ($\chi^2 = 14.82$, df = 1, $P \leq 0.001$). In 2006, VIT wing length was the same as in 2005, but we cut some antennas to a shorter length ($n = 21$, mean = 6.1 cm, SD = 0.6 cm, range = 5.1–6.9 cm), and we left some as standard from the manufacturer ($n = 23$, mean = 9.6 cm, SD = 0.2 cm, range = 9.3–9.9 cm). We classified 81% (17 of 21) of short-antenna VITs and 43%

(10 of 23) of long-antenna VITs as successful drops ($\chi^2 = 6.76$, df = 1, $P = 0.009$). However, we determined that at least 62% (8 of 13) of long-antenna VITs classified as unsuccessful were near parturition in time and space as evidenced by presence of a deer neonate during initial fawn searches and in 2 cases a birth-site as well (84 and 144 m from VIT drop-site). Similarly, we determined that 75% (3 of 4) of short-antenna VITs classified as unsuccessful drops were near parturition.

From June–August, 2004–2006, we estimated distance from birth-sites and time since parturition for 96 fawn captures. Of these, we had 33 incidences of twin captures resulting in a total sample of 63 observations (34 mule deer, 29 white-tailed deer). From the full model explaining *distance* moved away from birth-sites by neonates with explanatory effects of *age*, *species*, and *age*×*species*, we first removed the *age*×*species* interaction term (estimates = 0.14 ± 0.23 [1 SE], $P = 0.544$). The effects of log-transformed *age* (estimates = 1.35 ± 0.12 [1 SE], $P \leq 0.001$) and *species* (estimates = 0.44 ± 0.19 [1 SE], $P = 0.027$) demonstrated enough significance as partials that we left them in the final model explaining 70% of the variance (adjusted $R^2 = 0.691$). Our model predicted that after 24 h postpartum, white-tailed fawns were on average nearly 250 m from birth-sties whereas mule deer were about 150 m from birth-sites (Fig. 1). To find fawns within 100 m of a birth-site, our model predicted that on average, researchers should capture white-tailed and mule deer fawns within 12.5 and 17.5 h postpartum, respectively, although outliers may be expected (Fig. 1). The *species* effect may be spurious, but we felt it was justified to describe the deer at our study site based on field observations, and it may be related to a localized difference in maternal antipredator behavior between species (S. P. Haskell, unpublished data).

Of 118 hoof growth measurements, the weighted regression analysis considered 44 non-zero observations related to mortality events. We kept the full model (adjusted $R^2 = 0.871$) predicting *age* with covariates *new hoof growth*, *species*, and *new hoof growth*×*species* because the interaction term was significant (estimates = 1.32 ± 0.38 [1 SE], $P = 0.001$). Compared to previous models derived from captive white-tailed fawns, our model generally predicted greater fawn ages from hoof growth measurements (Fig. 2). Ninety-five percent prediction limits for age (days) at 2, 6, and 10 mm of hoof growth were 6.2–10.4, 21.3–26.2, and 35.1–43.4 for our white-tailed fawns, and 8.7–12.0, 18.1–23.0, and 26.4–35.0 for mule deer, respectively. Perinatal mule deer fawns appeared to have less hoof growth than white-tails in our study, but accrued hoof growth faster during their first month of life with similar expectations at about 14 days-old and 3.5 mm of growth (Fig. 2). Our white-tailed model predicted a similar rate of hoof growth as that of Sams et al. (1996), but due to greater perinatal measurements by Sams et al. (1996; i.e., different intercepts), our model predicted that fawns were about 10 days older (Fig. 2). In contrast, Haugen and Speake (1958) recorded perinatal measurements similar to ours, but their recorded rate of hoof growth was greater (Fig. 2). Our mule deer model compared to the model of Robinette et al. (1973) in a similar way as our white-tailed model compared to that of Sams et al. (1996). That is, rates of hoof growth were similar but perinatal measurements made by Robinette et al. (1973) were greater than those we made on free-ranging mule deer fawns resulting in a general 11.5-day age prediction discrepancy (Fig. 2).

DISCUSSION

Although Carstensen et al. (2003) reported acceptable success with VITs for white-tailed deer in Minnesota, Seward et al. (2005) recommended greater VIT wing length for elk (*Cervus elaphus*) in Kentucky. Researchers in Colorado had difficulties with VIT retention in Rocky Mountain mule deer (Bishop et al. 2007), and we concur that greater VIT wing lengths resulted in greater retention for both species at our site in west-central Texas. Although we did not explicitly analyze success rates within each species, those rates at least doubled from 2004 to 2005 for both species. Johnstone-Yellin et al. (2006) recommended longer VIT antennas based on behavior of captive does that did not orally remove their VITs. However, of 19 VITs recovered from free-ranging does, they found 0 near birth-sites (Johnstone-Yellin et al. 2006), suggesting that free-ranging does may have behaved differently than captive does by removing their VITs prematurely, as we observed in some of our deer prior to 2006. We support Johnstone-Yellin et al.'s (2006) results that VIT antennas protruding farther from the vulva were generally easier to hear, although topography can amplify or obscure reception. However, despite determining that most VIT drops classified as unsuccessful were near parturition in space and time, we suggest that to facilitate fawn captures it helps to locate the birth-site and recommend that VIT antennas not protrude >1 cm past the vulva to increase occurrence of successful drops. Also, a blunt epoxied tip on a VIT antenna may reduce fraying, mitigate irritation to the vulva, and draw less attention from the doe.

We provide evidence that adult females may move their fawns considerable distances from birth-sites within the first 24 h postpartum (Fig. 1). Our model predicts within 30 h postpartum when most data were recorded, but theoretically, the function should take an asymptotically logistic form over longer periods of time. Researchers should respond to birth events quickly to ensure neonate capture, but we had no success finding fawns in the dark using thermal imaging (Butler et al. 2006) or lights. Our results for white-tailed fawns in particular (Fig. 1) may be negatively biased, because on several occasions we investigated birth-sites within 4–12 h postpartum and failed to find any fawns despite searches (100% coverage objective) covering a 250–300-m radius.

There has been concern for marking-induced abandonment of fawns (White et al. 1972, Livezey 1990). Based on our observations and others' (Michael 1964, Truett 1977, Heffelfinger 2006:153, Johnstone-Yellin et al. 2006), we recommend waiting about 3 h before investigating an expelled VIT to allow the doe to birth, clean, and feed her young; variability may be expected. Researchers may monitor a doe's radiocollar and VIT from about 100–150 m away by telemetry to detect movement away from the birth-site and exercise prudence. We captured several viable fawns in and adjacent to birth-sites (*n* = 15, < 15 m from birth-sites) shortly after birth. We documented only 1 case of investigator-induced abandonment when we flushed a doe in labor (VIT expelled 3 h prior) that birthed her first of twin fawns about 10 m from her chosen birth-site while fleeing; the fawn was undersized and probably unviable, but the doe did not return. We radio-tracked doe and fawn locations intensively following captures. After adopting birth-site monitoring practices as suggested above, we were unable to document any abandonment due to our acute disturbance of the doe at birth-sites. However, we did experience losses due to fawns fleeing the capture site by several hundred meters and failing to reunite with their does (*n* = 4). We subsequently found that physically moving fawns back to the capture location could prevent such losses (*n* = 2). We concur with others (Carstensen Powell et al. 2005, C. Bishop, Colorado Division of Wildlife, personal communication) that risk of marking-induced abandonment was minimal and suggest that the critical bonding period between doe and fawn was limited to initial grooming and feeding immediately postpartum. We suggest that researchers determine marking-induced abandonment by intensive radiotelemetry monitoring rather than assuming responsibility for all early mortality events because some areas may have high early mortality naturally (Ricca et al. 2002, Pojar and Bowden 2004, Bishop et al. 2007).

Fawn aging models may be species-specific (Fig. 2). Furthermore, young mammals in captivity tend to grow more rapidly than free-ranging counterparts (O'Regan and Kitchener 2005), which could be the result of better nutrition in captive mothers or young (Sams et al. 1996, O'Regan and Kitchener 2005). This may explain the discrepancies between our model and those previously generated from captive fawns (Fig. 2). Also contrary to observations by Haugen and Speake (1958), we found that a fawn's umbilicus at our site could be dry within hours of birth. Behavioral, morphological, and physiological models derived from captive deer may be suspect when applied to free-ranging populations (this study; Carstensen Powell and DelGiudice 2005). Field biologists should be aware that previous growth models from captive fawns may predict positively biased growth estimates, or conversely, negatively biased age estimates based on field-collected morphometrics. These relationships may be site- and time-specific as well, so we encourage researchers to estimate their own growth models if possible. Variability in birth-date estimates could affect survival estimates from staggered-entry models, especially in a case study with high rates of perinatal mortality (Winterstein et al. 2001). Furthermore, underestimating fawn ages may give false security against potential early-survivor bias in overall survival estimates. The only way to know if such bias could exist may be to capture known-age neonatal fawns from birth-sites.

These observations on capturing and aging deer fawns should help researchers contemplating or engaged in fawn survival studies to execute successful operations and obtain sufficient reliable data. If applied properly, technological advances have potential to further our understanding of reproductive biology and juvenile mortality patterns and recruitment in wild ungulates. We caution against general use of models derived from captive deer to extrapolate inferences to free-ranging populations.

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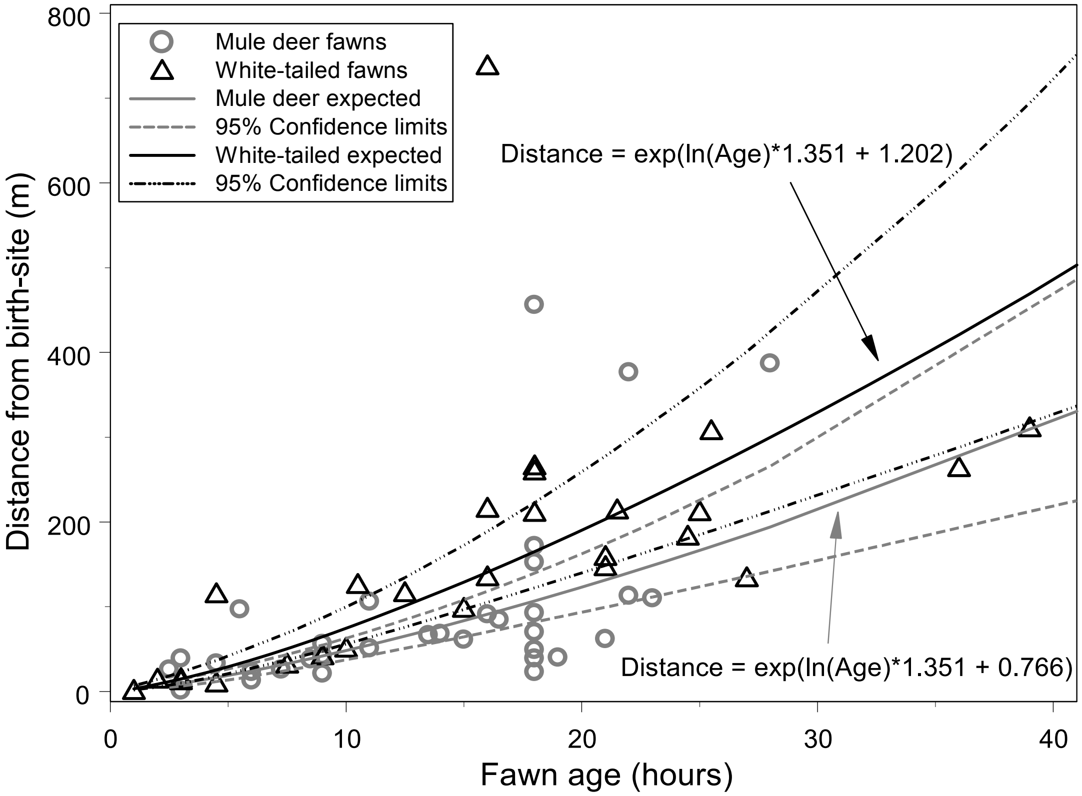

Figure 4.1. Distances white-tailed and mule deer fawns moved from birth-sites at time of capture as a function of age and species, west-central Texas 2004–2006. Predictive equation with log-transformed *age* effect only: Distance = exp(ln(Age)×1.346 + 0.973). Axes scaled to omit 3 observations > 48 hours-old for visual clarity of most data.

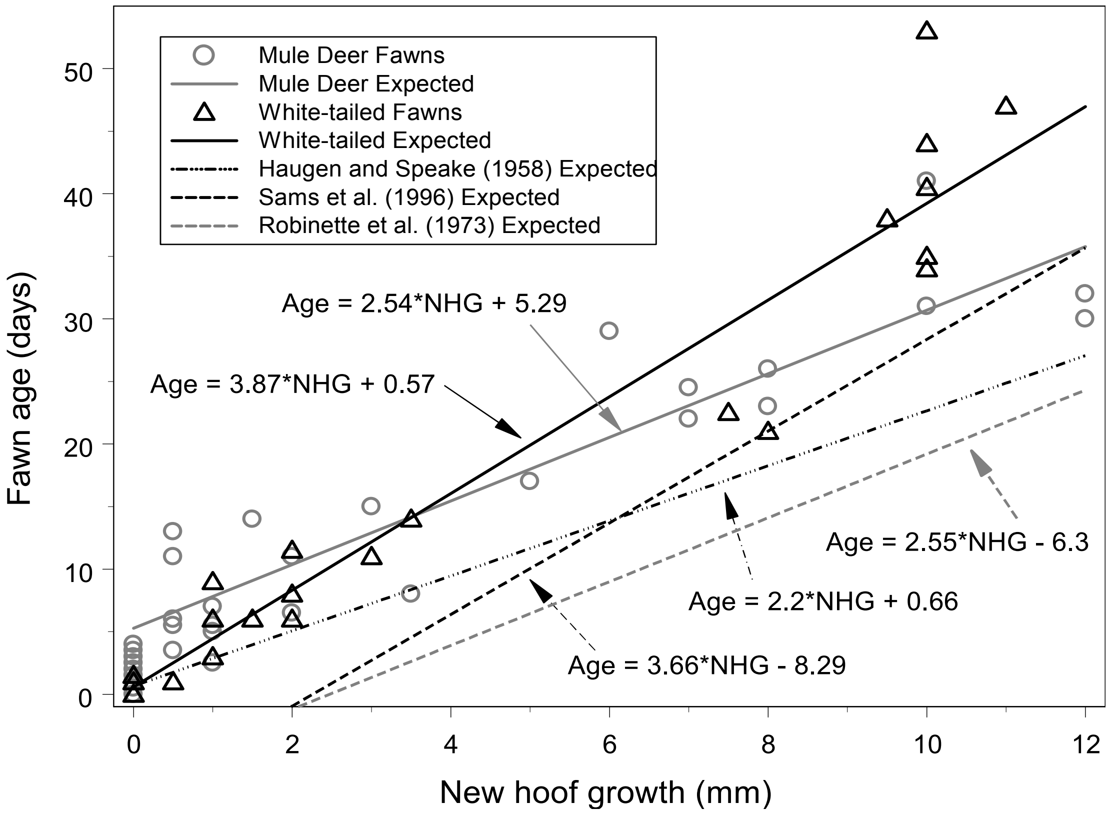

Figure 4.2. Known ages of white-tailed and mule deer fawns captured in west-central Texas from 2004–2006 versus new hoof growth measurements. Expectations from previous prediction models plotted for comparison against species-specific models from this study. Prediction limits for models from this study omitted for visual clarity (see Results).

CHAPTER V

FACTORS AFFECTING BIRTH DATES OF SYMPATRIC DEER IN WEST-CENTRAL TEXAS

Abstract: During the course of a fawn mortality study, we investigated proximate factors affecting birth dates of sympatric desert mule deer (*Odocoileus hemionus eremicus*) and white-tailed deer (*O. virginianus texanus*) in west-central Texas from 2004–2006. We treated this aspect of the case study as time-to-event survival (i.e., pregnancy to birth) and modeled the process with accelerated failure-time regression. Our best model included effects from 3 hierarchal levels: 1) within year variation among individuals within species, as older and heavier females birthed earlier, 2) among year variation at the population level, as greater rain during the previous pre-rut and rut periods resulted in earlier birthing, and 3) a chronic cohort effect also at the population level because even after previous effects were accounted for in regression models, deer birthed later on more overgrazed ranches. After accounting for weight, female age as a significant predictor may have indicated a behavioral phenomenon associated with social dominance. We did not find meaningful relationships between birth dates and either offspring gender or rain during gestation. Overall, Kaplan-Meier product-limit estimates indicated that white-tailed deer birthing peaked on 20 June (90% range = 31 days) and mule deer birthing peaked on 21 July (90% range = 45 days). We suggest that the 1-month separation between birthing and breeding periods of these sympatric deer species was due to some degree of phylogenetic constraint from parent populations and not localized adaptation with selection against hybridization. Prevention of genetic introgression may be a result by coincidence.

Key words**:** accelerated failure-time, birthing, individuals, *Odocoileus* spp, overgrazing, population, proximate factors, rain, sympatric, Texas

INTRODUCTION

Reproductive aspects of ungulate biology have been examined from an evolutionarily adaptive viewpoint (Millar 1977, Caley and Nudds 1987, Rutberg 1987, Ims 1990, Sheldon and West 2004). Resource pulses related to local climate affecting vegetative phenology can explain timing and synchrony of birthing seasons (Sinclair et al. 2000, Côté and Festa-Bianchet 2001, Post et al. 2003, Gogan et al. 2005, Loe et al. 2005), especially for species with hiding neonates such as those of *Odocoileus* (Geist 1974, 1998; Lent 1974; Rutberg 1987). In north-temperate species, there often exists a tradeoff in timing of parturition between plant emergence and the short growing season before onset of breeding and winter (Gaillard et al. 1993, Cook et al. 2004, Langvatn et al. 2004). Researchers have found considerable plasticity in birth seasons at sub-Familial levels (Clutton-Brock and Harvey 1984, Rutberg 1987, Rachlow and Bowyer 1994, Hass 1997) as well as some degree of phylogenetic constraint relative to variability in native or introduced local environments (Frädrich 1987, Hass 1997, Bowyer et al.1998, Asher et al. 1999, Locatelli and Mermillod 2005).

Our main focus was on proximate factors affecting birth dates of sympatric desert mule deer (*O. hemionus eremicus*) and white-tailed deer (*O. virginianus texanus*) within and among years. In general, improved nutrition results in earlier breeding and birthing

(Robinette et al. 1973). Poor nutrition during gestation can delay parturition (Verme 1965, Nilsen et al. 2004). Condition indices (e.g., body weight and rump fat thickness) measured pre- and post-partum may be correlated with breeding condition and have been negatively correlated with date of birth (Cameron et al. 1993, Birgersson and Ekvall 1997, Keech et al. 2000). Poor nutrition in the summer-autumn pre-rut and rut periods can be related to climatic conditions and can delay estrus, breeding, and parturition (Verme 1965, Adams and Dale 1998, Cook et al. 2001, Cook et al. 2004). Older females tend to ovulate earlier in the breeding season than younger females (Bon et al. 1993, Langvatn et al. 2004), and similarly, older females with high social status may breed and birth earlier than those of lower status, regardless of offspring gender (San Jose et al. 1999, Guilhelm et al. 2002, Holand et al. 2004*b*;).

Published results regarding offspring gender are more conflicting. Some accounts suggest that early breeding and birthing were associated with a predominance of male deer offspring (Hemmer 2006, Holand et al. 2006). Offspring gender may be affected by the male parent with dominant polygynous cervids breeding early and siring more males (Gomendio et al. 2006, Roed et al. 2007). However, birth dates may not accurately reflect breeding dates due to variable and possibly compensating gestation length (Berger 1992; Garcia et al. 2006, Holand et al. 2006). Studies of other ungulates have shown that female offspring were on average conceived or born earlier than males (Green and Rothstein 1991, Kruger et al. 2005). Young white-tailed deer bred later than older does and produced mostly male fawns, whereas older does "under the best nutritional circumstances" conceived more females (Dapson et al. 1979, Verme 1981, Ozoga and

Verme 1982:281). Another study of captive white-tailed deer demonstrated conception dates unrelated to offspring gender (DeYoung et al. 2004).

Lastly, populations with low abundance of adult males may exhibit later birth dates, presumably because females do not find suitable mates during first estrus (Komers et al. 1999, Holand et al. 2003, Saether et al. 2003). Also, it may be important to consider that individual or cohort differences among female offspring such as weight, dominance, and reproductive characteristics may persist through adulthood and may be passed to the next generation (Mech et al. 1991; Gaillard et al. 2000, 2003; Guilhelm et al. 2002; Hewison et al. 2005; Garroway and Broders 2005).

Our objective was to assess which aforementioned factors might have influenced birthing or breeding dates of sympatric deer on private lands in west-central Texas from 2004–2006, during a period with considerable variation in precipitation patterns. Prior to our study, we understood that white-tailed deer probably birthed earlier than mule deer (M. Humphrey, personal observation). We present a case in which neonates were captured from free-ranging does with data histories, so we were able to model individualistic as well as population-level effects. Body weight, fatness, and age may be good indicators of adult female social status as well as individual condition (Holand et al. 2004*a*, Veiberg et al. 2004, Vervaecke et al. 2005). For most fawns captured, we had measures of all three variables that were somewhat correlated with one another. We considered potential population-level effects of precipitation during the pre-rut–rut period and during gestation. Also, we considered a potential chronic nutrition effect because during field operations we observed that deer on the southern ranches tended to birth later than those on the northern ranches, and the southern ranches may have had a recent history of greater overgrazing resulting in less available forage. We did not examine a potential effect of adult sex ratios on birth dates because the deer population was lightly harvested, buck:doe ratios were consistent at 1 buck per 2.5 does, and pregnancy rates were high (S. Haskell, unpublished data).

STUDY AREA

Located in west-central Texas, our site was where the southwestern edge of the Edwards Plateau descends into the Trans-Pecos region (Fig. 1A). Heffelfinger et al. (2003) depicted this area as a semi-arid transition zone between the Great Plains and Southwest Deserts ecoregions. Elevations ranged from 870 m ASL on mesa tops to 750 m ASL along a central riparian corridor (Fig. 1C). The area was primarily a shrub-dominated community without tall canopy cover except in riparian areas. On average, January was the coldest month with high and low temperatures of 13°C and -2°C, and July was the hottest month with high and low temperatures of 34°C and 20°C (National Oceanic and Atmospheric Administration [NOAA] 2004). Normal annual rainfall was about 40 cm per year with peaks in May and September (Fig. 2). Other researchers have described the area in greater detail (Avey et al. 2003, Butler et al. 2006).

Land-use was primarily livestock ranching, but low-pressure lease hunting with some corn-feeding (Adams et al. 2004) and petroleum exploration and extraction also occurred. Roads varied from a paved county road to two-track unimproved ranch roads (Fig. 1C). Both white-tailed and desert mule deer were present at the site in near equal abundance at a combined density of about 30/km^2 in autumn 2005 (Haskell et al. 2008). The buck:doe ratio was about 1:2.5 (Haskell et al. 2008). 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). We conducted research on 4 contiguous private ranches encompassing a total of about 324 km^2, but our operations were within an area of about 100 km^2 (Fig. 1C).

METHODS

Field data

In April 2004–2006, we captured adult female deer using a net-gun fired from a helicopter (Holt Helicopters, Uvalde, Texas, USA; Krausman et al. 1985). We weighed each deer with a Hanson hanging scale and pulled a tooth for aging by cementum annuli after administering lidocaine as a local anesthetic (Matson's Laboratory, Milltown, Montana, USA; Swift et al. 2002, Mansfield et al. 2006). We estimated ingesta-free body fat content and pregnancy rates by ultrasonography (Smith and Lindzey 1982; Stephenson et al. 1995, 2002) and fitted each pregnant doe with a vaginal implant transmitter (VIT; ATS, Isanti, Minnesota, USA) and radiocollar (Telonics, Mesa, Arizona, USA and ATS, Isanti, Minnesota, USA). The VITs were used to help locate neonates for capture <24 hrs after birth (Carstensen et al. 2003). We used the precise-event codes from VITs, information from monitoring schedules, and evidence from birth-sites to estimate time of births within 0.5–10 hrs (Haskell et al. 2007). We also captured random fawns opportunistically; these were aged with a site- and species-specific aging model based on new hoof growth (Haskell et al. 2007). All field operations complied with Texas Tech University Animal Care and Use Committee permit # 03075-10.

To examine potential population-level responses of birth dates to environmental conditions, we retrieved precipitation data from 5 NOAA weather stations within 60 km from the center of our study site (NOAA National Climatic Data Center, Asheville, North

Carolina, USA). Clockwise from due north, these stations were located in Big Lake, Ozona, Sheffield, Bakersfield, and McCamey, Texas (Fig. 1B). We generated monthly averages among the stations, as rainfall in this region can often be localized. We summed the monthly averages from August–December 2003–2005 to represent the pre-rut and rut periods and from January–May 2004–2006 to represent the gestation periods associated with each birthing season. The NOAA data included a long-term departure-from-normal value associated with monthly rain totals; we used the departure-from-normal data to estimate normal rain patterns.

During our field investigations we noticed that births tended to be later on the southern ranches at our study site compared to the northern ranches. It became apparent to us that the southern ranches had received chronically greater overgrazing than the northern ranches (Fig. 1D). Results from vegetation cover-board surveys of fawn bed-sites in 2004 and 2005 indicated means of 40.3% (SE = 2.7%) cover on the northern ranches versus 31.2% (SE = 2.5%) cover on the southern ranches from 0–1.6 m above the ground in similar mesquite (*Prosopis glandulosa*)-tarbush (*Flourensia cernua*) habitats ($t = 2.44$, df = 102, $P = 0.017$; D. Butler, unpublished data). Thus, we hypothesized that even after annual variability in individual- and population-level effects were accounted for in regression models that a chronic inter-generational north-south site effect may still be present.

Data analysis

The process we wished to model was essentially time-to-event survival (i.e., pregnancy). Because we examined factors affecting the timing of the event (i.e., birth), we treated the process as an accelerated failure-time regression model (Fox 2001, Kalbfleisch and Prentice 2002, Kleinbaum and Klein 2005). We chose to model multiplicative failure times with the log-logistic distribution *a priori* because it has parsimonious flexible properties that allow zero initial hazard for some time (Fox 2001); *post hoc* comparisons of log-likelihood values and Kaplan-Meier plots confirmed our choice over alternate distributions or an additive-effect model (Fox 2001, Kleinbaum and Klein 2005). We initiated the survival period on 14 May each year, so model predictions began from this reference point.

We excluded adult marked females that gave birth at unknown dates because assigning right-censorship dates would have been subjective and unreliable. Also, we wished to begin the survival period in mid-May to minimize cumulative survivorship periods of 100%, thereby facilitating model fits. We would have had to right-censor several adult females prior to mid-May. Therefore, our dataset included uncensored information from captured fawns only, assuming that they were representative of the population.

The assumption of independence of observations was violated to some degree because in many cases we captured twin fawns, and some fawns were from the same does among years. We entered each twin into the dataset independently because it was necessary to do so to examine a potential sex effect on birth dates, and twin occurrence appeared unrelated to birth date; most fawns were in twin sets regardless. Also, capturing fawns from the same does among years gave us a unique opportunity to examine a potential age effect that could be considered a powerful repeated measure. Frailty models for clustered data were not available in SAS® 9.1 PROC LIFEREG (SAS Institute Inc., Cary, North Carolina, USA; Kleinbaum and Klein 2005). Thus, we tried to account for potential family effects using PROC NLMIXED (SAS 2004); initializing parameter estimates facilitated successful model convergence (Littell et al. 2006). We used the equations for the log-logistic survival and probability density functions given by Fox (2001) because the results matched those from PROC LIFEREG prior to addition of random effects. However, with no REPEATED statement available in PROC NLMIXED (Littell et al. 2006), we were unable to design an appropriate covariance structure, and results were spurious with large gradients for fixed parameters. Ultimately, we chose to model the process with fixed effects only in PROC LIFEREG understanding that standard errors and p-values from partial parameters may be underestimated, perhaps resulting in a tendency to overfit the data (Kalbfleisch and Prentice 2002).

There was ambiguity, correlation, and missing data in predictor variables, so we considered both information-theoretic (Akaike Information Criterion [AIC]) and frequentist statistics to define and asses an *a priori* model set (Burnham and Anderson 2002, Stephens et al. 2005). We presented an r-squared goodness-of-fit statistic (R^2_{LR}) based on likelihood ratios (Magee 1990). Doe weight and body fat were correlated (n = 87, $r = 0.27$, $P = 0.012$ for mule deer; $n = 49$, $r = 0.47$, $P = 0.001$ for white-tailed deer), but we were missing 2 observations for body fat, so we compared these 2 competing variables by partial p-values after finding a candidate model with doe weight by AICc. We plotted Kaplan-Meier cumulative survivorship curves using SAS PROC LIFETEST and S-Plus 7.0® (Insightful Corp., Seattle, Washington, USA) to help describe categorical covariate effects (Fox 2001, Kleinbaum and Klein 2005).

RESULTS

In each April 2004–2006 we captured and fitted 25 does of each species with VITs; in 2005 and 2006 we recaptured surviving does and replaced dead deer (*n*=1 and 9, respectively). All does were pregnant in 2004 and 2005, and 2 mule deer adults and 1 white-tailed short-yearling were barren in 2006. We captured 51, 59, and 59 fawns in 2004, 2005, and 2006, respectively. Of these, we removed 4 fawns from the analysis because we were unable to determine sex, as they were born as mummified fetuses (*n*=3) or already predated. We also removed 2 white-tailed fawns from the analysis because they were born from yearlings, which were themselves bred as fawns, and understandably were biological outliers having been conceived much later than other white-tailed fawns. The remaining 105 mule deer fawns and 58 white-tailed fawns were captured from 75 separate does. Of these 163 fawns, only 138 were captured from 54 separate does with known data histories including age and body weight at capture in April. An additional 2 fawns were from 2 marked does that were missing body fat data. We captured 25 fawns from 21 does that were not marked or handled by researchers, so we were unable to include these observations in any model considering individual doe characteristics. Overall, Kaplan-Meier product-limit estimates indicated that white-tailed deer birthing peaked on 20 June with 90% occurring within 31 days and mule deer birthing peaked on 21 July with 90% occurring within 45 days.

To simplify the model set we began with the full model including main effects of species, sex, location (north v. south), August–December precipitation, January–May precipitation, doe age, and doe weight along with an interaction term for species×August–December precipitation to test the hypothesis that the effect of precipitation depended on species. From this full model, we removed 1 variable at a time depending on lowest partial test statistic and highest p-value until reaching the fully-reduced intercept-only model. In sequential order we removed: the interaction term ($\chi^2_1 = 1.29$, $P = 0.258$), sex ($\chi^2_1 = 1.14$, $P = 0.287$), January–May precipitation ($\chi^2_1 = 1.31$, $P = 0.253$), doe weight ($\chi^2_1 = 5.53$, $P = 0.019$), doe age ($\chi^2_1 = 9.38$, $P = 0.002$), location ($\chi^2_1 = 10.55$, $P = 0.001$), August–December precipitation ($\chi^2_1 = 15.78$, $P \leq 0.001$), and finally, species ($\chi^2_1 = 280.19$, $P \leq 0.001$).

Consistent with the preceding information, model selection by AICc suggested that the model including doe weight along with subsequently discarded variables was best (Table 1). However, considering R^2_{LR} statistics, the partial p-value of January–May precipitation (given above) in model no. 2 (Table 1), and the issue of dependence in our data, we suggest that the second most plausible model should be simpler and not more complex. Model no. 5 (Table 1) would be the second most plausible model after removing doe weight from model no. 1 (Tables 1, 2). All other models seem relatively implausible. Substituting doe fat for doe weight in model no. 1 (Table 1) indicated that doe fat was not competitive ($\chi^2_1 = 0.07$, $P = 0.792$) even though somewhat correlated with doe weight. The preferred model (Table 1, no. 1) indicated that: 1) mule deer birthed later than white-tailed deer, 2) cumulative rain from the previous August–December was negatively related to birth date, 3) older and heavier does gave birth earlier, and 4) deer on the northern ranches gave birth earlier than those on the southern ranches (Table 2).

After accounting for the individual-level effects in the preferred model of doe age and doe weight (Table 1, no. 1), population-level effects were species, location, and

August–December rain. While the median birth date (from 14 May = 0) for white-tailed deer was earlier on the northern ranches (33.6 days; 31.1–37.5 95% CI) than on the southern ranches (40.6 days; 35.6–46.7 95% CI), the effect was not as strong for mule deer with 67.5 days (64.8–69.5 95% CI) in the north and 70.0 days (66.1–75.1 95% CI) in the south (Fig. 3). However, it was apparent that mule deer began their birthing season earlier in the north with 25% quartile estimates equal to 58.9 days (53.2–63.7 95% CI) in the north and 65.0 days (60.3–66.7 95% CI) in the south (Fig. 3). The birthing period appeared briefer on the southern ranches (Fig. 3).

The 2 species also responded to cumulative rain from August–December similarly (Fig. 4). Simple nonparametric mean birth dates (from 14 May = 0) in 2004, 2005, and 2006 were 39.7, 31.8, and 39.4 days for white-tailed deer and 69.3, 64.2, and 75.2 days for mule deer, respectively. Prior to the birthing seasons of 2004, 2005, and 2006, there was a total of 21.7 cm, 38.3 cm, and 19.5 cm of rain in August–December and 21.2 cm, 15.0 cm, and 6.9 cm of rain in January–May, respectively. The early birthing season of 2005 was associated with the most rainfall during the previous August–December among years (Fig. 4) but with the medium amount of January–May rainfall among years. The January–May rainfall data during gestation did not fit the birthing period data well.

DISCUSSION

We examined factors influencing birth dates of deer at 3 hierarchal levels: 1) within year variation among individuals within species, 2) among year variation at the population level, and 3) a chronic inter-generational effect also at the population level. We found evidence for effects at all 3 levels working simultaneously. The species effect alone explained most of the variation in birth dates (Tables 1, 2). After controlling for species, the factors influencing birth dates of deer at the same 3 respective hierarchal levels were: 1) doe age and doe weight, 2) cumulative rain during the pre-rut and rut periods from August–December of the previous year, and 3) location in a more or less overgrazed range.

With similar gestation periods (reviews by Demarais et al. 2000, Kie and Czech 2000), it is interesting that these species bred and gave birth about 1 month apart in sympatry. White-tailed and mule deer are reproductively compatible and frequently hybridize in contact zones but with limited introgression (Cronin 2003, Baker and Bradley 2006). However, with no predators at our site larger than foxes (*Urocyon cinereoargenteus* and *Vulpes vulpes*) or bobcats (*Lynx rufus*), reproductive isolation of these species was not likely pre-mating due to anti-predator habitat segregation or post-mating due to reduced fitness of F_1 hybrids with confused adult anti-predator behavior (Lingle 1993, 2002). Also, mule deer were extirpated from our study site sometime in the early–mid 1900s and have only recolonized and come into contact with white-tailed deer within the past 25 years (Schmidly 2004; L. D. Clark, ATA ranch manager, personal communication). Thus, it seems unlikely that the mean difference in breeding periods was the result of selection against hybrids or any other mode of species reinforcement (review by Servedio and Noor 2003).

It is possible that the presence of another similar species reduced the duration of the breeding period by some behavioral means. In all years combined, 90% of white-tailed birthing, and presumably breeding, occurred within 31 days at our site. Studies of nearby allopatric white-tailed populations in central and southern Texas indicated that 90% of conceptions occurred within about a 1.5-month period (Teer et al. 1965, Harwell and Barron 1975). An alternate hypothesis to explain this phenomenon may be that the birthing and breeding periods were reduced at our site because white-tailed deer were less ubiquitous throughout the area being mostly restricted to lowlands (Avey et al. 2003, Brunjes et al. 2006), thus making estrous females more accessible to breeding males. In contrast, mule deer, while selecting mesa habitats, used all habitats at our site (Avey et al. 2003, Brunjes et al. 2006). Their birthing period was more extended with 90% occurring within 45 days overall while exhibiting larger tails in distribution, and particularly so on the northern ranches with greater relative abundance and interspersion of mesa habitats (Figs. 1C, 3).

We suggest that the difference in mean birthing periods between species was more likely due to some degree of phylogenetic constraint, as both species appeared to be synchronized with parent populations. Mule deer at our site were of the *eremicus* subspecies adapted to the environments and precipitation regimes of the semi-arid and arid southwestern United States. Southwestern deer such as *O. h. eremicus*, *O. v. couesi*, and *O. v. carminis* tend to birth during July and August in synchrony with summer rains from convective storms (review by Heffelfinger 2006). In contrast, the white-tailed deer at our site likely had origins to the north and east having expanded their range westward in the early 1900s after overgrazing and fire suppression caused brush encroachment into grassland-savannah habitats (Teer et al. 1965, Wiggers and Beasom 1986, Van Auken 2000). In southern Illinois and central Texas, allopatric populations of white-tailed deer had peak birthing periods near mid-June (Teer et al. 1965, Nelson and Woolf 1985). Thus, while the 1-month separation in peak birthing periods for these sympatric species may help prevent genetic introgression, it is likely a coincidence not associated with localized adaptation by natural selection. The bimodal distribution of rain with peaks in May and September may help maintain the dichotomous birthing pattern (Fig. 2).

After individual doe weight was accounted for in the regression model, doe age was still a significant factor (Tables 1, 2). It is well understood that females in better condition may enter estrus, breed, and birth earlier than those in poorer condition (Verme 1965, Robinette et al. 1973, Adams and Dale 1998, Cook et al. 2001, Cook et al. 2004), but how age relates to breeding biology beyond the correlation with body condition is less clear. The relationship may be physiological and behavioral (Bon et al. 1993, San Jose et al. 1999, Guilhelm et al. 2002, Langvatn et al. 2004, Holand et al. 2004*b*). Regardless of weight, female age may be positively correlated with social status (Townsend and Bailey 1981), and reproductive senescence may not occur in *Odocoileus* (DelGiudice et al. 2007). Agonistic dominance encounters during the rut are usually associated with male deer (Geist 1981, Marchinton and Hirth 1984, DeYoung et al. 2006, Hoem et al. 2007, Johnson et al. 2007), but such behavior can occur among females as well (Bergerud 1974). Côté and Festa-Bianchet (2001) found no maternal effects of age or social rank on birth dates of mountain goat (*Oreamnos americanus*) kids, but mountain goats occupy more northern and seasonal environments and are more gregarious, so breeding and birthing periods with less variance may be expected. It is possible that during the rut mature males first tended older and mature females that exhibited dominance over younger females, and that younger subordinate females have adapted to delay first estrus until a few days after that of dominant females for fawn-rearing advantages related to postpartum deer behavior or predator swamping (Ozoga et al. 1982, Ozoga and Verme 1986, Nixon and Etter 1995, Aycrigg and Porter 1997, Whittaker and

Lindzey 1999). Alternatively, behavioral interference may have caused some young deer to remain barren after their first estrus. Such hypotheses remain difficult to test in free-ranging conditions, but our data were suggestive of a behavioral effect associated with doe age.

Similar to McGinnes and Downing (1977), we found that population-level environmental influences on birth dates operated prior to conception and not during gestation. Cumulative rain during the pre-rut and rut periods correlated well with mean birth dates (Fig. 4), but rain during the gestation period did not. Furthermore, if we were to treat white-tailed and mule deer in separate models, we would stagger those periods by 1 month. Assuming gestation periods of 205 days, the peak of breeding for white-tailed and mule deer at our site would have been near the last day of November and December, respectively. Removing the rain data for December from the relationship to white-tailed deer birth dates would have no real effect on a similar analysis (Fig. 2), but removing the August data from the mule deer analysis would cause a relative increase of total rain in 2003 and improve the fit of the data (Fig. 4). McGinnes and Downing (1977) found delayed birthing after relatively high fawn survival from the previous year, presumably because lactation demand in does successfully rearing fawns may result in relatively poor condition and delayed breeding in autumn. However, from 2004–2006, our population of deer experienced greatest fawn recruitment from the 2004 cohort prior to the earliest birthing period in 2005 (Fig. 4, S. Haskell, unpublished data). Thus, deer at our site may invest less energy rearing fawns and seemed more influenced by variability in rain pre-conception.

Land-use practices that alter wildlife behavior and resource use patterns may or may not affect population parameters (Cronin et al. 1998, Mallord et al. 2007). On average, deer on the northern ranches birthed earlier than those on the southern ranches (Fig. 3; Tables 1, 2). After accounting for individual- and population-level variability within and among years (Table 2), this remaining effect may indicate an inter-generational phenomenon related to greater overgrazing on the southern ranches. Digestibility of forage plants used by white-tailed deer was lower on grazed plots compared to ungrazed plots except in summer (Thill et al. 1987), and inter-generational or cohort effects are not unknown (Mech et al. 1991; Gaillard et al. 2000, 2003; Guilhelm et al. 2002; Garroway and Broders 2005; Hewison et al. 2005). Also, contiguous deer populations have previously demonstrated different demographics due to localized relationships to vegetative carrying capacities (Dapson et al. 1979), and others have suggested that reduced deer and livestock densities can shift peak breeding to an earlier date (Demarais et al. 2000). With different land use practices (i.e., grazing pressure) on neighboring properties that outsize deer home-ranges substantially, it is plausible that demographics could differ across a fence-line (Fig. 1D). It is not yet known if vital rates such as fawn production and survival were also altered by these land use differences (e.g., Taylor and Hahn 1947, McMahan 1964, McMahan and Ramsey 1965, Hailey et al. 1966), or if by adjusting breeding and birthing dates, the deer have adequately compensated for chronic poorer nutrition in this mild-winter environment; we will investigate this further in the future.

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Table 5.1. Accelerated failure-time regression models explaining variability in birth dates of sympatric white-tailed and mule deer fawns in west-central Texas, 2004–2006. Parameters are species (1), fawn gender (2), location (3), cumulative rain from August–December of the previous year (4), cumulative rain from January–May (5), doe age (6), doe weight (7), and a species×August–December rain interaction term (8). Models had an identical response set (*n* = 138). Statistics include likelihood-ratio based goodness-of-fit (R^2_{LR}), model log-likelihood, number of estimated parameters (K), and model selection by information-theoretics (AIC).

Model	Parameter(s)	R^2_{LR}	Log(L)	K	AIC	AICc	ΔAICc	w_i
1	1,3,4,6,7	0.76	30.17	7	-46.33	-45.47	0.00	0.42
2	1,3,4,5,6,7	0.76	30.82	8	-45.63	-44.52	0.95	0.26
3	1,2,3,4,5,6,7	0.76	31.38	9	-44.77	-43.36	2.11	0.15
4	1,2,3,4,5,6,7,8	0.77	32.02	10	-44.05	-42.32	3.15	0.09
5	1,3,4,6	0.75	27.41	6	-42.82	-42.18	3.29	0.08
6	1,3,4	0.73	22.68	5	-35.36	-34.90	10.57	0.00
7	1,4	0.71	17.59	4	-27.17	-26.87	18.60	0.00
8	1	0.68	10.13	3	-14.25	-14.07	31.40	0.00
9	intercept-only	0.00	-68.20	2	140.40	140.49	185.96	0.00

Table 5.2. Type III analysis of effects for the preferred model explaining birth dates of sympatric white-tailed and desert mule deer fawns in west-central Texas, 2004–2006. Parameters include species, location (north vs. south ranches), cumulative rain from August–December of the previous year (cm), doe age at conception (yrs), and doe weight at April capture during gestation (kg). For categorical variables of species and location, white-tailed deer and the southern ranches, respectively, were set as the zero reference values. Statistics include maximum-likelihood parameter estimates with standard errors (SE), 95% confidence limits, chi-squared test value (χ^2, *df* = 1), and p-value. For predictions with this log-linked model, effects must be summed before being exponentiated with 14 May = 0.

Parameter	Estimate	SE	LCL	UCL	χ^2	Pr > χ^2
Intercept	4.351	0.189	3.982	4.720	533.03	≤0.001
Species	0.698	0.041	0.618	0.779	289.05	≤0.001
Location	-0.124	0.034	-0.189	-0.058	13.71	≤0.001
Aug–Dec rain	-0.006	0.002	-0.010	-0.003	10.76	0.001
Doe age	-0.028	0.008	-0.044	-0.012	11.91	0.001
Doe weight	-0.009	0.004	-0.016	-0.001	5.53	0.019

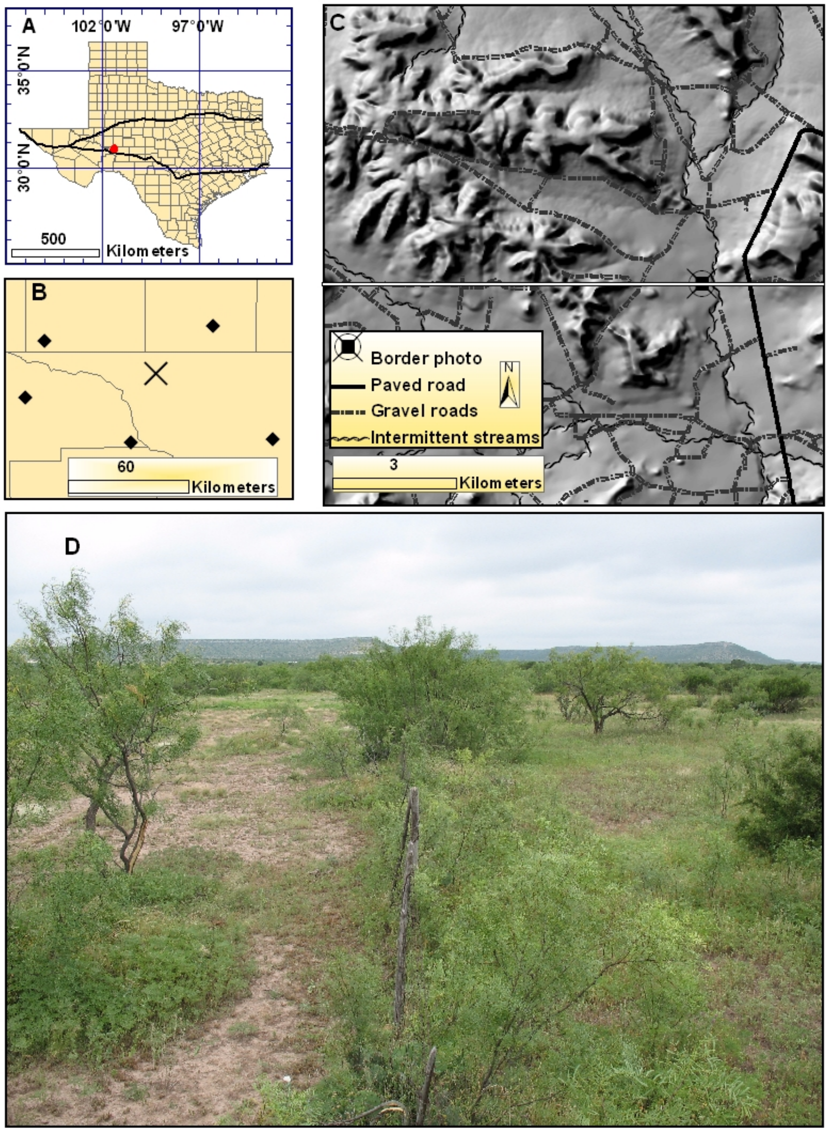

Figure 5.1. Site for study of sympatric white-tailed and desert mule deer in west-central Texas, USA, 2004–2006, including: A) location in northwest Crockett County near interstate highway no. 10, B) location of 5 NOAA weather stations around the study area, C) shaded relief of the study area with horizontal line delineating north ranches from south ranches, and D) north-south fence-line photo taken on 29 June 2007 from east to west. South ranch appears more overgrazed than north ranch.

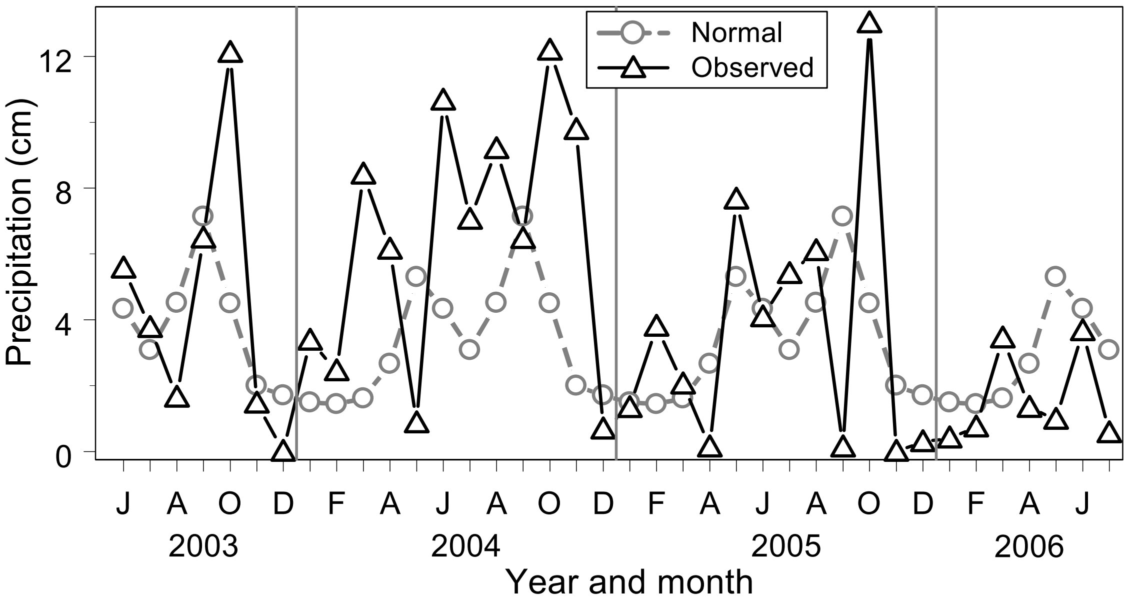

Figure 5.2. Monthly precipitation patterns averaged from 5 NOAA weather stations located at Big Lake, Ozona, Sheffield, Bakersfield, and McCamey, Texas, June 2003–July 2006, versus average normal precipitation. Precipitation form was nearly 100% rain. Vertical lines delineate years.

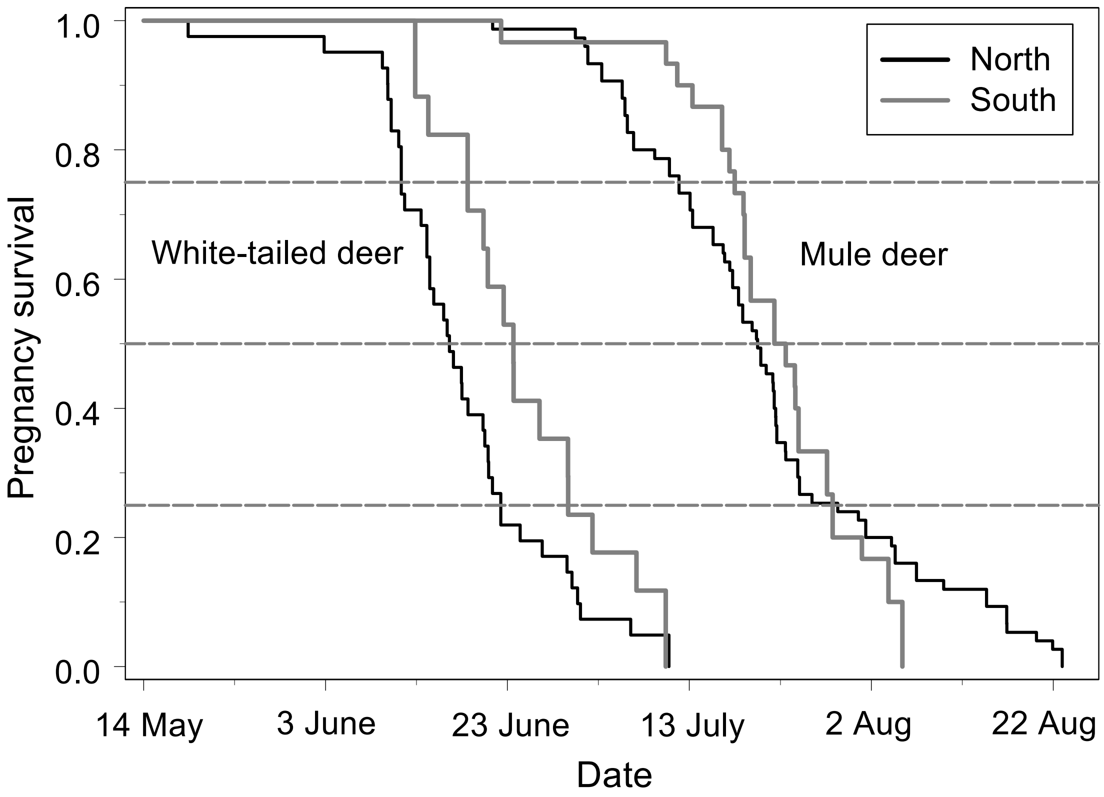

Figure 5.3. Kaplan-Meier product-limit cumulative survival estimates of pregnancy for sympatric white-tailed and desert mule deer in west-central Texas, 2004–2006, as influenced by ranch location and associated land-use practices. Horizontal lines intercept curves at quartile estimates.

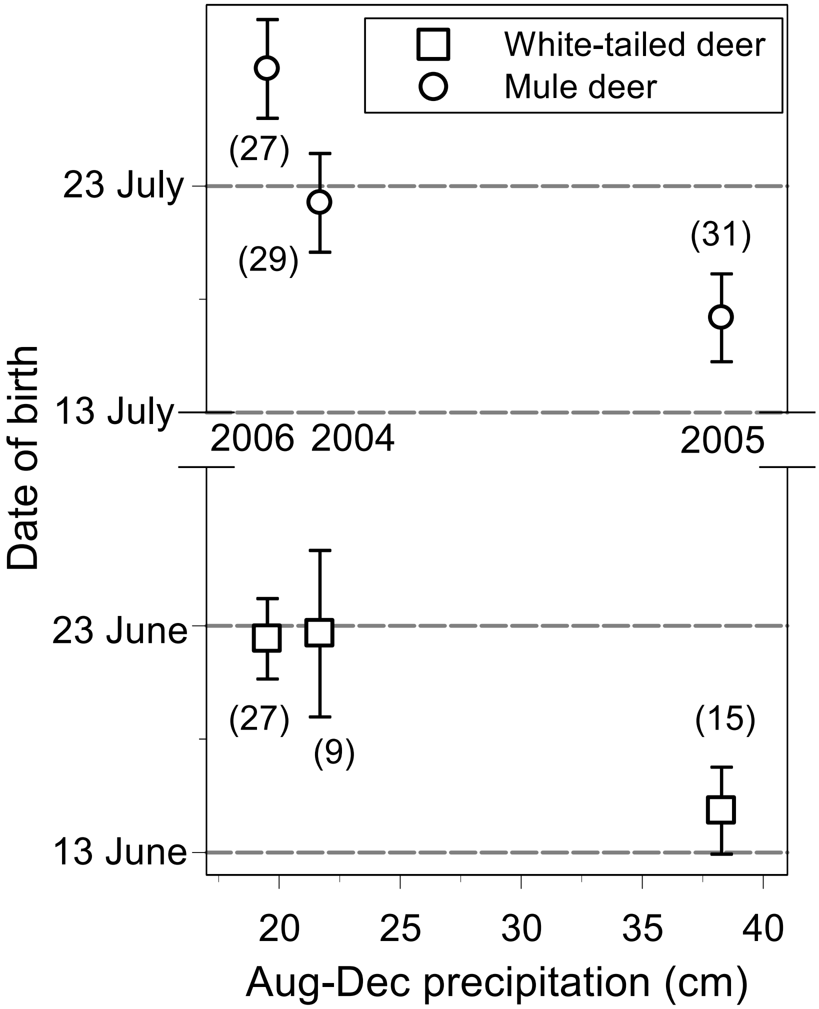

Figure 5.4. Kaplan-Meier product-limit mean estimates (±1 SE) of white-tailed and mule deer birth dates in 2004–2006 influenced by cumulative precipitation from August–December of the previous year. Year labels correspond to summer birthing periods. Sample sizes in parentheses. Horizontal dashed lines for Y-axis reference and note Y-axis break; above and below scaled identically.

CHAPTER VI

PRODUCTIVITY, MORTALITY, AND ANTIPREDATOR STRATEGIES OF FEMALE AND FAWN DEER IN WEST-CENTRAL TEXAS: A TALE OF 2 SPECIES

Abstract: Understanding deer demographics and behavior in sympatric contact zones is of ecological and management interest. Between the mid-1800s and -1900s, mule deer (*Odocoileus hemionus eremicus*) were extirpated from most of their range in west Texas after anthropogenic brush encroachment into native habitats and concomitant westward range expansion of white-tailed deer (*O. virginianus texanus*). The preferred hypothesis to explain the west-Texas mule deer decline was that converted habitats were less suitable for mule deer, thus facilitating competitive exclusion by white-tailed deer. However, in the past 25 years, mule deer have recolonized many areas from the west, once again coming into contact with white-tailed deer in similar habitats as those previously abandoned. Our study was in one such area of northwest Crockett County, Texas. The area had a history of livestock ranching, and of the 4 ranches we studied, the 2 southern ranches were more overgrazed by cattle only, and the 2 northern ranches were less overgrazed but had both sheep and cattle in most pastures.

Previous research at our site indicated that mule deer used all habitat types while white-tailed deer avoided mesa habitats. We examined: 1) sympatric adult female mortality from 2000–2002 during a period of prolonged drought, and 2) productivity, mortality, and antipredator behavior of adult females and fawns from 2004–2007 during a period that began wet and became progressively drier. Although our study was

observational by nature, we formulated *a priori* hypotheses and relied on variable rain patterns to create a natural experiment. In 2004 and 2005, nearly all adults tested positive for hemorrhagic disease antibodies in sera and negative for bovine viral diarrhea and infectious bovine rhinotracheitis. Parainfluenza and bovine respiratory syncytial virus appeared more prevalent in mule deer but were also present in some white-tailed deer. Overall, vitamins A and E and selenium appeared sufficient. In 2004, we obtained reliable age data for adult females, and there appeared to be a positive bias for mule deer yearlings in our sample captured by net-gun, thus emphasizing the potential need to control for this variable by inclusion in regression modeling. Reproductive rates for both species were high in 2004 and 2005 with 100% pregnancy, and most with twins. Productivity was reduced for both species in spring 2006. Adult mule deer were heavier than white-tailed deer, deer weights increased to 6 years-old at which time they decreased, and both species weighed less in spring 2006 than in 2004 and 2005. The cause of reduced weights and productivity in 2006 may have differed by species; we suggest 6 months of dry weather for white-tailed deer and pathogens related to the substantial rains of 2004 for mule deer.

From about 300 adult deer-years, we recorded 1 bobcat (*Lynx rufus*) kill, 1 hunter kill, 3 poacher kills, 2 road kills, 12 sickness-starvation mortalities, and 12 unknown causes of death; top-down limitation was negligible. For survival analyses, we used Kaplan-Meier estimates for exploration and description of simplified categorical covariates and Cox proportional hazards for likelihood-based hypothesis testing. Seasonal periods of reduced survival were from August–mid-October and mid-November–February, representative of the lactation and weaning period and the rut and post-rut period, respectively. During the drought period of May 2000–2002, mule deer survival (0.98, 0.96–1 95% CI) was higher than that of white-tailed deer (0.82, 0.73–0.92 95% CI). As predicted, white-tailed deer survival (0.92, 0.87–0.98 95% CI) increased in the wetter period from May 2004–2007, but unexpectedly, mule deer survival (0.87, 0.80–0.94 95% CI) decreased, exhibiting a lagged response after the phenomenal rainfall of 2004. We hypothesized *post hoc* that reduced mule deer survivorship following much rain may have been due to increased viral vectors such as *Culicoides* midges and an environment more conducive to growth and transmission of bacteria and other pathogens associated with livestock that were also increased.

From 2004–2006, we used vaginal implant transmitters to catch 145 fawns from adult females with data histories and 25 fawns from unknown females. Most fawns from known females were captured from birth sites at <1 day-old, but fawns from unknown females were a median of 6 days-old. Most singletons were female, and males were prevalent on the southern ranches. After controlling for fawn age at capture, relatively heavy adults produced heavy fawns, mule deer were heavier than white-tailed fawns, singletons were heaviest, and fawn weight decreased with adult female age. Fawn weights were lowest in 2004, which given rain patterns, suggested female condition at breeding was an important factor. The fawn age effect indicated weight gain of 0.06 kg/day for 1 week postpartum; weight gain appeared to increase for older fawns but was still low.

We omitted 6 known fawns from survival analyses due to likely investigator-induced mortality. Best models explaining fawn survival included covariates relying on data from known adult females, so we omitted 25 other observations from analyses.

Most mortality occurred <45 days postpartum. Overall survival of the 139 fawns was 78% by 6 days-old, and ranged annually from 50% in 2004-05 to <20% in 2006-07. There were 47 mortalities by sickness-starvation, 47 by predation, 1 other cause, and 3 undeterminable. Diseases appeared diverse. Bobcats were responsible for nearly all predation (approx 30% of fawns) with the latest recorded mortality at 282 days postpartum. We found no evidence for a behavioral carrying capacity, as adult female age did not predict fawn survival after accounting for other effects. Relative fawn weight was more important near birth, and gender became important ≥30 days postpartum, at which time males were at greater risk of sickness-starvation. Skewed sex ratio at recruitment matched adult ratios. The Lunn-McNeil competing risks models suggested some interaction between sickness-starvation and predation (i.e., direct compensatory mortality). Reduced rain during the May–August late gestation and lactation period increased rates of sickness-starvation and predation. Overall, mule deer fawns succumbed more to sickness-starvation, and weaning data suggested that it was disease and starvation that primarily afflicted fawns on northern and southern ranches, respectively. Rates of sickness-starvation and predation increased with deviance from mean birth dates. Thymus gland and fawn weight data indicated that bobcat predation was additive mortality, but bobcats were known to kill at least 2 prematurely weaned fawns <16 days-old, suggesting that some mortality was directly compensatory. Furthermore, because fawn depredation was the greatest top-down limiting factor for this deer population, bobcat predation may alleviate density-dependent effects in good rain-years, thus becoming to some degree indirectly compensatory at a broader ecological scale.

We collected postpartum group cohesion telemetry data in 2004 and 2005. During the fawns' hider phase, mule deer females kept fawns closer to themselves (39–66 m, 95% CI) and twins closer to each other (25–49m, 95% CI) than did white-tailed females (152–234 m, 95% CI, and 163–255 m 95% CI, respectively). After 4 weeks postpartum, familial group cohesion was tight for both species. During hider phases from 2004–2006, white-tailed fawn carcasses (11 of 11) were dismembered or consumed more than mule deer fawns (8 of 13, $P = 0.041$), which we cited as 1 line of evidence for maternal defense by mule deer adults. Mule deer fawn carcasses appeared consumed more in 2006 when adult females were in worst condition and fawn survival was lowest. During the hider phase in 2004 and 2005, predation rate of mule deer fawns (10%, 5–21% 95% CI) was lower than that for white-tailed fawns (19%, 9–38% 95% CI). In 2006, predation rate of mule deer (28%, 15–49% 95% CI) increased but remained similar for white-tailed fawns (21%, 11–41% 95% CI). The tight cohesion strategy of mule deer exhibited in 2004 and 2005 seemed successful at thwarting some predation, but predators were more successful in 2006. In the absence of large predators, the loose cohesion strategy of white-tailed females was maladaptive, perhaps the result of a relatively long evolutionary history with many large predators.

Data from adult female weights and survival and fawn survival, thymus glands, weight gain, new hoof growth, birth dates, and weaning dates indicated that this deer population was chronically stressed near a carrying capacity that fluctuated with rain and that females invested relatively energy in rearing fawns. We suggest that it was pathogens introduced by livestock ranchers that were responsible for the historic decline of a naïve mule deer herd in west Texas. Mule deer appear to have developed some

immunity, but even in the best of rain-years, mule deer fawns succumbed mostly to sickness-starvation. Mule deer may eventually achieve enzootic stability similar to white-tailed deer. Human use of these private lands and the unhealthy deer herd has been consistent for decades and likely will remain so. Responsible deer management is impossible where human land-use practices affect ecology and demographics across fence-lines and top-down limitation is negligible. We recommend research into alternative economic means and public ecological education of youth and adults as the management action with greatest potential for desirable results.

***Key words*:** behavior, cause-specific mortality, disease, fawns, maladaptive, mule deer, *Odocoileus hemionus eremicus*, overgrazing, *O. virginianus*, predation, rain, starvation, Texas, white-tailed deer.

INTRODUCTION

North American *Odocoileus* deer are important economically via hunting and recreation (Demarais et al. 2000, Kie and Czech 2000), culturally as iconic wildlife (Heffelfinger 2006, Heffelfinger et al. 2006), and ecologically as potential dominant species capable of altering vegetative structure and community relationships (DeCalesta 1994, Hobbs 1996, Stromayer and Warren 1997, Côté et al. 2004, Wisdom et al. 2006). Overabundance may also cause concerns for agricultural depredation, automobile collisions, and disease transfer (McShea et al. 1997, Schwabe and Schuhmann 2002). Management objectives and biological considerations typically vary at regional and local scales (Wallmo 1981, Halls 1984, McCullough 1987, deVos et al. 2003).

In many areas of western U.S., deer declines perceived in the mid–late 1900s may have followed artificially high deer densities after population bonanzas in the early 1900s; deer appeared scarce to early western pioneers prior to predator control campaigns, range conversions from grass to browse, and water development in xeric regions (Leopold et al. 1947, Julander and Low 1976, Urness 1976, Clements and Young 1997, Van Auken 2000, Krausman et al. 2006). Therefore, managers responsible for deciding local objectives to appease wildlife stakeholders must consider history, habitat conditions, human land-use practices, and predatory influences on deer demographics.

Where predators have been reduced (Cahalane 1939, Hairston et al. 1960, Taber and Raedeke 1987, Skogland 1991, Hayes et al. 2003, Bergerud et al. 2007), forage limitation may be the primary constraint on deer populations in many regions of North America (Teer et al. 1965, Solterogardea et al. 1994, Patterson and Power 2002, Stewart et al. 2005, Binkley et al. 2006). Poor nutrition is reflected by a deer herd via decreased body weights and low reproductive and survival rates, particularly for juveniles (Gaillard et al. 2000). Density-dependent and -independent factors such as weather, behavior, predation, disease, and parasites may interact to cause such responses (Connelly 1981, Fryxell and Sinclair 2000, Miller and Wentworth 2000, Marshal et al. 2002, Murray et al. 2006).

While population dynamics of ungulates are most sensitive to relatively constant adult female survival rates, juvenile recruitment tends to be the most variable demographic vital rate, ultimately having the greatest effect on population trajectory (Skogland 1990; Gaillard et al. 1998*a*, 2000; Unsworth et al. 1999; Garrott et al. 2003; Haskell and Ballard 2007*a*). Predation may be the major cause of fawn mortality in many white-tailed and western mule deer herds (Hamlin et al. 1984, Fox and Krausman 1994, Kunkel and Mech 1994, Whittaker and Lindzey 1999, Lingle 2000, Ballard et al. 2001, etc.), but starvation can be an important factor affecting both adult and fawn survival (White et al. 1987, Ricca et al. 2002, Lawrence et al. 2004, Pojar and Bowden 2004).

By understanding environmental influences on deer demographics, managers may gauge the relationship between a deer herd and its variable carrying capacity and possibly make predictions useful for hunting regulations. Winter is considered to be the seasonal energetic bottleneck for deer in the northern temperate regions (Mautz 1978, Moen 1978, Ballard et al. 1991, Delgiudice et al. 2002, Bishop et al. 2005). However, for parous females and concomitant neonates in xeric habitats of southwestern U.S., the energetic bottleneck occurs during the spring and summer months during periods of late-gestation, lactation, and hot temperatures that can cause dry conditions and forage die-off without ample precipitation (Anthony 1976, Brown 1984, Demarais et al. 1986, Lautier et al. 1988, Leopold and Krausman 1991). Even at more northern temperate latitudes, summer and autumn nutrition may affect reproduction and recruitment (Julander et al. 1961, Pederson and Harper 1978, Cook et al. 2004), although reproduction may be more affected for polytocous species that attempt to maximize energy assimilation and realize potential fecundity (Schoener 1971, Haskell and Ballard 2004).

We conducted our study of sympatric white-tailed (*O. virginianus texanus*) and desert mule deer (*O. hemionus eremicus*) in a semiarid environment of west-central Texas. Ecological studies of similar species in sympatry may yield unique insight into fundamental differences within the context of a natural experiment “controlled” in space and time.

Adult Female Survival

In xeric southern temperate climates, severity of the dry season or long-term drought can affect adult female survival in ungulates (Fryxell 1987, Lawrence et al. 2004). Adult female survival of desert mule deer in southwest Texas increased as the region transitioned from a period of drought to wetter conditions (Lawrence et al. 2004). The primary sources of mortality were natural stress and predation, occurring mostly during summer months, but natural stress losses appeared to decline at a greater rate than did predation losses as the wet period increased in longevity (Lawrence et al. 2004). In areas where stochastic environmental processes cause variability in adult female survival independent of predation, such variability may be clear indication that that the population experiences intermittent chronic stress near an ecological carrying capacity (Teer et al. 1965, Gaillard et al. 2000, Miller and Wentworth 2000).

Despite similar diets (Krausman 1978), studies in the western U.S. have shown that coexistence of mule and white-tailed deer within sympatric range may be facilitated by differential habitat selection where topography and vegetation associations are heterogeneous (Martinka 1968, Kramer 1973, Anthony and Smith 1977, Wood et al. 1989, Brunjes et al. 2006). Morphological (e.g., larger ears and thinner tails) and observational evidence suggests that mule deer in southwestern U.S. are better adapted to hotter and more xeric environments than are white-tailed deer (Geist 1998, Heffelfinger 2006). Drought had greater impact on demographic vital rates of Coues white-tailed deer (*O. v. couesi*) than those of desert mule deer (Anthony and Smith 1977). A series of spring droughts appeared to result in local extirpations of Coues deer in the Sonoran Desert of Arizona (Brown and Henry 1981). Similarly, Carmen Mountains white-tailed deer (*O. v. carminis*) in Big Bend National Park, Texas, were absent from more xeric areas between natural water springs, and after water tanks went dry, mule deer were the only species present on mesas that previously held white-tailed deer (Krausman and Ables 1981). Therefore, we predicted that adult female survival of white-tailed deer would demonstrate greater response to variable precipitation than that of mule deer females at our study site.

Fawn Mortality and Recruitment

Aerial survey data from northwest Crockett County, Texas, in winters 1999 and 2001 indicated fawn:female ratios of 0.5:1 and 0.23:1 for mule deer and 0.43:1 and 0.18:1 for white-tailed deer, respectively (K. J. Brunjes and W. B. Ballard, Texas Tech University, unpublished data), although individuals of both species usually produce twins (Demarais et al. 2000, Kie and Czech 2000). These ratios were similar to ratios recorded in the Trans-Pecos region of Texas during the 1980s and were within or lower than the range of reported ratios for other deer herds in southwestern U.S. (Carroll and Brown 1977, Smith and LeCount 1979, Pittman 1987). Variability in autumn fawn:female ratios are probably not due to conceptive failures (Robinette et al. 1957*a*, Barron and Harwell 1973, Carroll and Brown 1977, Hamlin et al 1984, Andelt et al. 2004). Relative abundance of west-Texas fawns in fall counts was positively correlated with precipitation the previous spring, but it was unknown if the proximate link to early fawn survival was vegetation as it affected adult female and fawn nutrition or hiding cover from predators

(Ginnett and Young 2000). Thus, there appeared to be a need for data regarding cause-specific fawn mortality.

Without direct evidence, exploitative forage limitation has been presented as the causative mechanism affecting fawn survival rates due to density-dependent processes (McCullough 1979, Fowler 1981, Picton 1984, Clutton-Brock et al. 1987, Bartmann et al. 1992). Alternatively, a density-dependent response in early fawn survival of a supplementally-fed white-tailed deer herd may have indicated a more obscure causative mechanism associated with postpartum territorial behavior of females (Ozoga and Verme 1982, Ozoga et al. 1982). Prime-aged (i.e., ≥4 years-old at parturition) females may lose fewer fawns due to their higher social status, and younger subordinate females may lose fawns due to inabilities caused by interference, psychological stress as it affects physiology, or increased predation risk after being relegated to marginal habitats, regardless of nutrition (Ozoga et al. 1982; Ozoga and Verme 1984, 1986*a,b*). Others have described territorial behavior of supplementally-fed and free-ranging North American *Odocoileus* that could affect recruitment (Miller 1974, Woolf and Harder 1979, Gavin et al. 1984, Dusek et al. 1989, Nixon and Etter 1995). Maternal interference in overpopulated deer herds could also compromise neonatal (i.e., <1 day-old) immunocompetence by reduced suckling and passive absorption of maternal antibodies from critical colostrum (Robbins et al. 1987, Sams et al. 1996). Such phenomena could influence a behavioral carrying capacity along with the traditionally understood K-carrying capacity determined by relative forage abundance (Miller and Wentworth 2000). Prime-aged multiparous females may have greater rearing success with less temporal variability than younger or older females (Guinness et al. 1978, Clutton-Brock 1984, Ozoga and Verme 1986*b*, Dusek et al. 1989, Kunkel and Mech 1994), but we are unaware of any existing data that show this relationship uncoupled from body condition in individual free-ranging deer.

With few exceptions (e.g., Kunkel and Mech 1994, Carstensen Powell et al. 2005, Bishop et al. 2007), most North American free-ranging fawn survival studies did not include fawns from marked females with recent and repeated data histories. These few studies usually documented little fawn mortality due to causes other than predation, suggesting that the deer herds were below K-carrying capacity. Also, most previous researchers did not locate fawns from actual birth sites (e.g., Dickinson et al. 1980, Huegel et al. 1985, Ballard et al. 1999, Brinkman et al. 2004, Vreeland et al. 2004, Pusateri Burroughs et al. 2006, etc.), and therefore, may have estimated positively biased survival rates if neonate mortalities occurred within a few hrs of birth (Murphy and Coates 1966, Verme 1977, Gaillard et al. 2000, Andelt et al. 2004). This would be of particular concern if females were in poor condition or in dense concentrations (Verme 1962, Ozoga et al. 1982) with abundant scavengers (Cook et al. 1971, Krausman and Ables 1981).

With recent improvements to the design and function of the vaginal-implant transmitter (VIT; Bowman and Jacobson 1998, Carstensen et al. 2003, Haskell et al. 2007), researchers may now have better success locating birth sites and true neonates, thus obtaining relatively unbiased fawn survival estimates (Linnell et al. 1995). Risk of marking-induced abandonment appears minimal but should be monitored carefully (Linnell et al. 1995, Carstensen Powell et al. 2005, Bishop et al. 2007, Haskell et al. 2007). Studies that follow individuals’ rearing success across years (e.g., repeated measures) may better define the relationships between the potential influences of nutritional limitation and social status along with environmental correlates and predation.

Maternal Antipredator Strategies

The importance of understanding animal behavior for implementing sound management practices has been recognized for over 50 years (Dasmann and Taber 1956, Geist and Walthers 1974). Mule deer and white-tailed fawns begin life as inactive hiders for 3–4 weeks postpartum, relying solely on nutrition from the female that visits the fawn 1–3 times daily for feeding and grooming (Lent 1974; Geist 1981; Marchinton and Hirth 1984; Hirth 1985, 2000). At about 2 weeks-old, fawns begin to forage for short periods, and they become functional ruminants by about 8 weeks-old (Short 1964, Jackson et al. 1972).

These species share other behavioral similarities, but differences also exist. Despite the gregarious nature of mule deer relative to white-tailed deer, females of both species often isolate themselves and their fawns from conspecifics for about 1 month postpartum (Hawkins and Klimstra 1970, Krämer 1973, Ozoga et al. 1982, Riley and Dood 1984). Pre- and postpartum maternal aggression towards other females and yearlings has been noted in white-tailed deer (Hirth 1977, Ozoga et al. 1982), black-tailed deer (*O. h. columbianus*; Miller 1974), and mule deer (Koutnik 1981, Riley and Dood 1984). At extremely high or low local densities, deer may exhibit greater tolerance (Michael 1964, Krämer 1973, Bowyer et al. 1998).

Although born in the same location, white-tailed siblings were separated at birth from usually >125 m apart and may not be present together until 3–4 weeks-old, at which time the female may again permit a yearling’s presence (Downing and McGinnes 1969, Jackson et al. 1972, White et al. 1972, Ozoga et al. 1982, Carstensen Powell et al. 2005). Triplet siblings were an average of 162 m apart during their first 2 weeks of life; this distance steadily decreased to 30 m by 8 weeks-old (Ozoga et al. 1982). Separation of twin fawns may have survival value by reducing the likelihood of a large predator finding both fawns (Jackson et al. 1972, White et al. 1972, Lent 1974). White-tailed fawns may begin following their dam at 3–4 weeks-old (Demarais et al. 2000).

Relatively little is known about mule deer postpartum grouping. Twins may be found together within a day or 2 from birth, and adult females may be nearby or absent (Truett 1977, 1979; Geduldig 1981). Of 7 doe-fawn groups examined, females were 10 m–1.8 km from fawns; 76% of female radiolocations were within 250 m of the fawn (Riley and Dood 1984). Only 1 study has examined social patterns of mule and white-tailed deer fawns where they existed sympatrically. Marked mule deer fawns in southern Alberta had more frequent associations with other marked fawns as winter progressed, whereas white-tailed fawns generally did not associate with other marked fawns despite overlapping home ranges, suggesting a temporal factor of shared space during this life stage (Lingle 2003). Remote studies using methods such as radiotelemetry can accrue spatial data for fawns during the initial postpartum hider phase without affecting animal behavior by observation.

Mule deer evolved in more open habitats than white-tailed deer, and in conjunction, the 2 species adapted different antipredator strategies (Geist 1981, Lingle and Wilson 2001). Adult mule deer reduced predation risk from coyotes (*Canis latrans*) by forming larger groups and aggressively confronting the attacker, whereas white-tailed deer fled to cover and used speed for evasion (Lingle 2001, Lingle and Pellis 2002).

White-tailed and roe deer (*Capreolus capreolus*) females appeared to favor a separate-and-hide antipredator strategy for their fawns but have been noted to attack predators such as coyotes and foxes (*Vulpes vulpes*) when discovered near their fawn (White et al. 1972, Jarnemo 2004). If maternal rearing strategies mimic adult antipredator behaviors, mule deer females may be more likely than white-tailed deer to defend their fawns from attack by predators; thus, it may be advantageous for mule deer to keep their fawns close together and nearby. This type of behavioral correlation across situations has been termed a behavioral syndrome and has been used to explain behaviors that appear maladaptive in an isolated context (Sih et al. 2004).

During our first summer of fawn captures in 2004, we noticed that white-tailed fawns were difficult to find even by locating adult females and birth sites, and twins were rarely found near each other. In contrast, when mule deer began birthing about 1 month later, we usually found twin fawns closer to birth sites and one another, with the dam nearby (Haskell et al. 2007, 2008*a*). We hypothesized that: 1) the tight postpartum group cohesion observed for mule deer would continue through the fawns' hider phase, 2) tight cohesion for mule deer was an antipredator defense strategy, and 3) in the absence of large predators, the loose postpartum group cohesion strategy of white-tailed deer was maladaptive.

In summary, in the absence of appreciable top-down limitation (see Study Area), the sympatric deer herds in northwest Crockett County likely exists at or above a carrying capacity that responded to rain. Female deer at this site may invest relatively little energy rearing fawns (Haskell et al. 2008*a*). Desert mule deer may be less susceptible to drought than are white-tailed deer. Density-dependent and -independent processes limit ungulate populations that are sensitive to adult female survival but are primarily affected by variable juvenile recruitment. Exploitative forage limitation is usually assumed to be the density-dependent proximal mechanism that affects demographics, but empirical evidence is usually lacking, and hypotheses for an alternate socio-behavioral mechanism have not been tested. Postpartum white-tailed and mule deer females may exhibit aggression towards conspecifics, but mule deer are more aggressive towards predators and may be more apt to keep fawns close for antipredator defense. Predation, particularly by generalist canids and ursids, is the most common source of fawn mortality in communities with predators, but starvation can be a significant source of mortality, and disease usually plays a minor role (Linnell et al. 1995).

To examine the validity of our hypotheses (Table 1), our objectives were to determine the following: 1) survival rates and cause-specific mortality of radiocollared white-tailed and mule deer adult females during drought and wet periods, 2) weather patterns, 3) condition and age of adult females prior to parturition, 4) reproductive rates, 5) fawn weights and gain rates, 6) unbiased fawn survival and causes and patterns of mortality, 7) thymus gland characteristics and stomach contents from dead fawns, 8) simultaneous radiolocation data within postpartum familial groups, and 9) fawn kill-site characteristics. Our study was observational by nature, so we relied on natural environmental variability to create experimental conditions for testing of research hypotheses (e.g., density-dependence as related to a changing carrying capacity) rather than manipulating the populations of interest and assuming a constant environment (Scheiner 2001).

STUDY AREA

Our study site was located in northwest Crockett County, Texas, where the western edge of the Edwards Plateau breaks down into the Trans Pecos desert in a transition zone between the Great Plains and Southwest Deserts ecoregions (Heffelfinger et al. 2003, Fig. 1). Elevations ranged from 750 m ASL along a central riparian corridor to 870 m ASL on mesa tops (Fig. 1). On average, July was the hottest month with high and low temperatures of 34°C and 20°C, and January was the coldest month with high and low temperatures of 13°C and -2°C (National Oceanic and Atmospheric Administration [NOAA] 2004). The area was semiarid with most precipitation occurring during summer convective storms that were often localized (Teer et al. 1965, Schmidly 2002). Averaged from 5 NOAA weather stations <60 km from the study site, normal annual rainfall was about 41 cm per year with peaks in May and September and a dry period from November–April (Figs. 2, 3; Haskell et al 2008*b*).

This region has a history of livestock grazing by cattle, goats, and sheep and extensive predator control to protect those human interests (Teer et al. 1965, Cook 1984, Teer 1984, Schmidly 2002). By 1900, the open-range grazing system had changed to stock farming with barbed wire fencing and drilled wells for stock water tanks (Schmidly 2002). The area is almost entirely private lands. All large predators (e.g., canids, felids, and ursids) have been extirpated with the exception of coyotes (*Canis latrans*) in many areas (Cook 1984; Schmidly 2002, 2004). Also by 1900, fire suppression and overgrazing by livestock resulted in widespread rangeland conversions from grassland-savannahs to shrub-dominated communities (Johnston 1963, Teer et al 1965, Severson 1981, Van Auken 2000, Schmidly 2002). White-tailed deer followed the expanding brush habitats westward from central Texas (Taylor and Hahn 1947, Teer et al. 1965, Wiggers and Beasom 1986). Between the mid-1800s and -1900s, mule deer disappeared from much of their original range in west Texas, receding westward (Cantu and Richardson 1997; Schmidly 2002, 2004). There has been speculation about effects of habitat fragmentation and hybridization (Schmidly 2004), but the preferred hypothesis to explain the decline of mule deer in west Texas was that unsuitable habitat conversion for mule deer facilitated competitive exclusion by white-tailed deer (Wiggers and Beasom 1986, Cantu and Richardson 1997). However, within the past 25 years, mule deer have recolonized parts of their original range that are still overgrazed and brush-dominated, including our study site, and have come back into contact with white-tailed deer in many areas (Wiggers and Beasom 1986, Kamler et al. 2001, Avey et al. 2003, Haskell et al. 2008*b*; L. D. Clark, former ATA ranch manager, personal communication).

Data from aerial surveys conducted in 1998 and 2002 during a period of drought indicated that abundance of mule deer relative to white-tailed deer had increased at our study site to about a 1:1 ratio (Texas Tech University, unpublished data). Mean annual precipitation from 1963–1997 was about 43 cm but was only 32 cm from 2000–2002 (NOAA 2004; Fig. 2). In contrast, the area received about 77 cm of precipitation in 2004, which was 1 of the wettest years in west Texas history since 1895 (NOAA 2004); some lifelong residents (1 >80-yr-old man) believed that they had never seen the range so green in August (L. D. Clark, former ATA ranch manager, personal communication). The Edwards Plateau and Trans Pecos regions underwent a prolonged period of moderate drought from 1993–2003. The annual mean of monthly Palmer Drought Severity Index (PDSI, Palmer 1965) values was -0.17 (± 0.19 SE) from 1895–2007 but was -1.34 (± 0.41

SE) from 1993–2003. Much of 2000 was classified as severe or extreme drought by the PDSI as a continuation of conditions from 1999 (Fig. 3). Heavy rains in October 2003 were the beginning of the end of the prolonged drought (Figs 2, 3). After the phenomenal rains of 2004, 2005 saw average rains that were decent during spring and summer but again became droughty in November which continued through much of 2006 (Figs. 2, 3).

Habitats were brush-dominated, principally by juniper (*Juniperus pinchotii*) on mesa tops and by mesquite (*Prosopis glandulosa*) on lowlands. Mesas were characterized by rim rock and rocky slopes. North-facing mesa slopes were also dominated by juniper and were more mesic than south-facing slopes. South-facing slopes were more open with lechugia (*Agave lechugia*), sotol (*Dasylirion texana*), and *Yucca* spp. (Fig. 1). A creosote (*Larrea tridentata*)-tarbush (*Flourensia cernua*) community was prevalent on well-drained lowland soils. Prickly pear (*Opuntia* spp.), cholla (*O. imbricata*), tasajillo (*O. leptocaulis*), acacia (*Acacia greggi*), algerita (*Mahonia trifoliolata*), and lotebush (*Ziziphus obtusifolia*) were also throughout lowlands and less so on slopes. A variety of forbs and grasses were present throughout the site at varying quantities. Streams were intermittent, becoming inundated briefly during severe summer storms. Riparian corridors supported thicker and taller herbaceous growth along with thickets of hackberry (*Celtis laevigata*) and walnut trees (*Juglans microcarpa*). White-tailed deer generally avoided mesa tops while mule deer used all habitat types perhaps with some selection for mesas (Avey et al. 2003, Brunjes et al. 2006, Butler et al. 2008).

Extirpation of large predators can release populations of mesopredators and small herbivores (Henke and Bryant 1999). Coyotes and larger predators were absent from our study site. The United States Department of Agriculture Wildlife Services was most active at our site in autumn 2006 when they killed >100 bobcats (*Lynx rufus*) by helicopter gunning from an area <150 km^2. Small–medium-sized mammals that appeared abundant, and perhaps overabundant, at our site were field mice (*Peromyscus* spp.), kangaroo rat (*Dipodomys* sp.), woodrat (*Neotoma* sp.), cotton-tailed rabbit (*Sylvilagus* sp.), black-tailed jackrabbit (*Lepus californicus texianus*), nine-banded armadillo (*Dasypus novemcinctus*), collared peccary (*Dicotyles tajacu*), hog-nosed skunk (*Conepatus mesoleucas*), striped skunk (*Mephitis mephitis*), opossum (*Didelphis virginiana*), porcupine (*Erethizon dorsatum*), raccoon (*Procyon lotor*), gray fox (*Urocyon cinereoargenteus*), red fox (*Vulpes vulpes*), and bobcat. Vultures (mostly *Cathartes aura* but some *Coragyps atratus*) were abundant during summers, and great-horned owls (*Bubo virginianus*) seemed abundant during summer 2005.

Our study site consisted of 4 contiguous private ranches encompassing 325 km^2, of which our deer were centrally located within about 90 km^2 during 2004–2007 (Fig. 1). The study area was larger prior to 2004. Human uses included livestock ranching (cattle, sheep, or both), lease hunting (Wiggers and Rootes 1987), and petroleum exploration and development. Stocking rates varied by land-holder, and many pastures were not grazed rotationally. Harvest rates of female white-tailed deer in the area were consistently below those recommended by Texas Parks and Wildlife Department biologists to maintain the deer herd below carrying capacity (Teer 1984; Texas Parks and Wildlife Department, unpublished data). Mule deer harvest had been buck-only for many years. Since1970, total harvest in Crockett County has been stable, but white-tailed deer density estimates declined from the mid-1970s through the mid-1990s and have stabilized since (Texas Parks and Wildlife, unpublished data). In November 2005, total deer density within the range of our fawn mortality study was near 30 deer/km^2, but this value may reflect relatively high local abundance in this sympatric range (Fig. 1; Haskell et al. 2008b). Males constituted the majority of the harvest with <1 deer/4 km^2 taken annually (S. Haskell, personal observation).

Competition for forage between overabundant deer, livestock, and lagomorphs was probably significant (Taylor and Hahn 1947, Julander 1955, McMahan 1964, Teer et al. 1965, Loft et al. 1991), and deer may have benefited from anthropogenic water sources and feeding of corn and minerals associated with lease hunting and ranching, respectively (Fig. 1; Rosenstock et al. 1999, Brown and Cooper 2006). Given such anthropogenic advantages coupled with poor range conditions and negligible top-down limitation, the deer herd in northwest Crockett County likely existed near some carrying capacity that fluctuated with precipitation (Fautin 1946, Teer 1984, Goldberg and Turner 1986, Jacobson and Kroll 1994, Haskell et al. 2008*a*).

METHODS

Rain and Drought Data

We retrieved precipitation data from 5 NOAA weather stations within 60 km from the center of our study site (NOAA National Climatic Data Center [NCDC], Asheville, N.C., USA; http://www.ncdc.noaa.gov/oa/ncdc.html, accessed 1 June 2007). Clockwise from due north relative to our study site, these stations were located in Big Lake, Ozona, Sheffield, Bakersfield, and McCamey, Texas (Haskell et al. 2008a). Precipitation was almost exclusively in the form of rain. Because rainfall in this region is often localized, we generated monthly averages among the stations and estimated normal values from the departure from normal data (Fig. 3). We summed the monthly averages from May–

August, September–December, and January–April to represent periods of late gestation and lactation, pre-rut and rut, and early–mid gestation, respectively, as vegetative response to rain in semiarid environments can occur within 2 weeks, particularly during the spring and early summer growing seasons (Smith and LeCount 1979; Wang et al. 2003; Weiss et al. 2004; Ji and Peters 2003, 2005; Pettorelli et al. 2005).

Drought and climate indices have been correlated with deer vital rates (Marshal et al. 2002, Haskell and Ballard 2004, Lawrence et al. 2004), so we explored for predictive capabilities of the PDSI and a related moisture anomaly index (ZNDX). The Palmer Drought Severity Index reflects long-term trends in drought conditions, while ZNDX accounts more for precipitation deficits and surpluses within the most recent 4 weeks and therefore is less serially autocorrelated (Palmer 1965). Monthly index values were available for the Edwards Plateau and Trans Pecos regions (NOAA NCDC), so we used the mean of the 2. Upon initial inspection of Palmer Index data, we identified the ZNDX as being more representative of summer range conditions we witnessed, as it tracked rain patterns closer than the PDSI (Figs. 2, 3).

Field and Lab

In February 2000 and 2001 and April 2004–2006, we captured adult female white-tailed and mule deer using a net-gun fired from a helicopter (Holt Helicopters, Uvalde, Tex., USA; Krausman et al. 1985). In 2000 and 2001, deer were radiocollared (Telonics, Mesa, Ariz., USA) and released at the capture site after estimating age by tooth-wear and replacement (Severinghaus 1949, Robinette et al. 1957*b*). In 2004–2006, deer were hobbled, blind-folded, and slung to a central processing location within 10 km of the capture site. In 2005 and 2006, we recaptured surviving adults and replaced mortalities to maintain a sample size of 25 for each species. We determined that all recaptured deer successfully returned to their prior home ranges after capture.

During handling in 2004–2006, we monitored deer temperatures and cooled by providing shade and spraying iced water externally and rectally if needed; we also permitted deer to drink. We weighed each deer with a Hanson hanging scale and pulled a last incisor (i.e., I4 canine tooth) for aging by cementum annuli (Matson's Laboratory, Milltown, Mont., USA; Gilbert 1966, Dimmick and Pelton 1996, Swift et al. 2002, Mansfield et al. 2006). We estimated pregnancy rates and ingesta-free body fat content by ultrasonography (Smith and Lindzey 1982; Stephenson et al. 1995, 2002) using an Aloka SSD-500V unit (Aloka Inc., Tokyo, Japan). We fitted each adult female with a radiocollar (Telonics, Mesa, Ariz., USA and Advanced Telemetry Systems, Inc., Isanti, Minn., USA) and those pregnant with a VIT (Advanced Telemetry Systems, Inc., Isanti, Minn., USA; Bishop et al. 2007). We recorded morphometrics and took ear-punch tissue samples preserved with lysis buffer solution. We archived tissue samples at the Museum of Texas Tech University. In 2004 and 2005, we drew blood intravenously, stored the samples on ice, and centrifuged. We handled each adult deer in about 10–14 min.

In 2004, we tested serum for bovine viral diarrhea (BVD), infectious bovine rhinotracheitis (IBR), parainfluenza (PIV-3), and bovine respiratory syncytial virus (BRSV) with serum neutralizing antibody titers (SN) and epizootic hemorrhagic disease (EHD) and bluetongue (BT) antibodies by agar gel immunodiffusion; we also estimated concentrations of vitamins A and E and selenium (Arizona Veterinary Diagnostic Lab, Tucson, USA; Howerth et al. 2001, Van Campen and Early 2001). In 2005, we repeated blood tests for EHD, BT, vitamin E, and selenium (Texas Veterinary Medical Diagnostic Lab, Amarillo, Tex., USA).

We conducted fawn searches from late May through late August in 2004–2006, as white-tailed deer birthing peaked near 20 June, and mule deer birthing peaked 1 month later (Haskell et al. 2008a). Our crew usually consisted of 4 people. We used the VITs to help locate birth sites and capture true neonates <24 hrs after birth (Carstensen et al. 2003, Bishop et al. 2007, Haskell et al. 2007, Butler et al. 2008). We used evidence from birth sites and neonates found to refine our fecundity estimates by ultrasonography (Haskell et al. 2007, Butler et al. 2008). We monitored VIT very high frequencies (VHF) daily from the ground between 00:00–07:00 hrs to preclude false-negative signals caused by direct sunlight on expelled VITs. Occasionally, we captured fawns from unknown females and aged those fawns with a site- and species-specific model based on new hoof growth (Haskell et al. 2007). We attempted to use thermal infrared imaging to locate known and random fawns with no success (Butler et al. 2006). We captured fawns by hand, placed in a cotton pillowcase, weighed and took body measurements, took a tissue sample from an ear treated with a topical triple-antibiotic gel, and fitted with an expandable 68-g VHF radiocollar (Diefenbach et al. 2003; Advanced Telemetry Systems, Inc., Isanti, Minn., USA). We handled each fawn in about 5 min.

We monitored deer survival by VHF pulse-rate at least daily from May–August, weekly through October, bi-weekly through December, and monthly through April. Also, fawn collars were equipped with a precise-event code (PET) that permitted estimation of when a collar stopped moving within 30 min for a period of 5.5 days prior to observing the fast-pulse mortality signal. We performed field necropsies and determined causes of death using methods described by Wade and Bowns (1984), Roffe et al. (1996), and Davidson and Nettles (1997). Thymus atrophy can be indication of physiological stress in deer fawns (Ozoga and Verme 1978, Verme and Ullrey 1984, Pojar and Bowden 2004), so we collected thymus glands opportunistically, stored them in an airtight freezer bags, and weighed with a Denver Instrument M-310 electronic scale with calibrated weight variance equal to 0.9 mg. When possible, we examined stomach contents for evidence of weaning. Pathology can be complex and results from field diagnostics should be considered as tentative hypotheses without direct pathogen isolation (Wobeser 1994, 2006; Davidson and Nettles 1997; Williams and Barker 2001). While we speculate and report on more proximate causative agents, for cause-specific analyses we simplified and categorized causes of death as predation, sickness-starvation, and other and undetermined.

We monitored radiocollars and conducted radiotelemetry with a telescoping dual 4-element yagi null-peak system (Balkenbush and Hallett 1988). We marked telemetry stations and recorded locations of sighted deer with a handheld global positioning system (model GPS 76; Garmin Inc., Olathe, Kansas, USA) with real-time accuracy of <5 m. We performed a radiotelemetry beacon study (*n* = 76) to generate a regression model for predicting linear errors of location estimates using covariates related to signal strengths, triangulation geometry, and distances (Withey et al. 2001, Haskell and Ballard 2007*b*, S. Haskell, unpublished data); we estimated GPS location error to be 5 m. MATLAB® 6.5 (The MathWorks, Natick, Mass., USA) files for triangulation location estimation and beacon study data are available at http://www.rw.ttu.edu/haskell/ (accessed 9 June 2007).

All field operations complied with Texas Parks and Wildlife Scientific Permit No. SPR-0404-363 and Texas Tech University Animal Care and Use Committee Permit No. 03075-10.

Analyses

General Modeling Procedures.— In most cases of regression modeling, we compared models with information-theoretic and other likelihood-based goodness-of-fit statistics (e.g., R^2_{LR}, Magee 1990; Burnham and Anderson 2002, Johnson and Omland 2004) but also presented estimated parameter coefficients, standard errors, and test statistics when appropriate to more thoroughly interpret results (Stephens et al. 2005, Murray et al. 2006). We simplified comparative model sets by starting with the fully-parameterized global *a priori* model, followed by single-term deletions according to lowest partial test statistic or interaction terms less significant than main effects, ending with the fully-reduced model. We also included other models of particular comparative interest. In accordance with the effect heredity principle, we retained insignificant partial parameters until a corresponding interaction term was removed (Neter et al. 1996, Nelder 1998). We examined potentially useful covariates with missing data by partial parameter statistics after introduction into the best model determined by Akaike's Information Criterion with second-order bias correction (AICc; Burnham And Anderson 2002). We used SAS® 9.1 (SAS Institute Inc., Cary, N.C., USA) for statistical modeling, S-Plus® 7.0 (Insightful Corp., Seattle, Wash., USA) for data plots, and MATLAB 6.5 for estimating radiotelemetry locations and performing randomized procedures.

Adult Capture.— We described the ages of adult females and reproductive rates from 2004–2006 and blood results from 2004 and 2005 with simple statistics. We used

PROC MIXED for repeated measures modeling (Littell et al. 2006) of adult weights as a function of year, species, age, age^2, and year×species in case older deer lost weight or an annual effect depended on species. Also, because the southern ranches appeared more overgrazed than the northern ranches and grazing pressure may affect deer biology at this study site (Haskell et al. 2008a), we considered a north versus south ranch fixed effect; we will continue to do so in other related analyses. We assumed a normal distribution of residual errors and a compound symmetry covariance structure, as the annual lag-time should have allowed little serial autocorrelation. We used maximum likelihood estimation for parameter estimates and Satterthwaite's method for estimating partial degrees of freedom (SAS 2004, Littell et al. 2006). We verified our choice of covariance structure versus unstructured and AR(1) by restricted maximum likelihood and comparing AICc (Littell et al. 2006). We compared fixed effects among models with AICc given by SAS although such statistics were approximations in these mixed effects models (Burnham and Anderson 2002, SAS 2004). We used the number of individuals as a conservative estimate of sample size for R^2_{LR} calculations (Magee 1990).

Adult Female Survival.— We began survival periods on 1 May each year, leading into the summer period associated with parturition and lactation that may be most stressful for female deer in this semiarid region (Lawrence et al. 2004, Haskell et al. 2008a). We did not include deer that died within 3 weeks of capture because of possible myopathy. From 2004–2006, we included deer from the 2000 and 2001 captures that remained alive with functional collars. We censored deer on the last date they were heard and assumed non-informative censorships that were probably best explained by collar failure given average home ranges of only 2.5 km^2 (Haskell et al. 2008b).

To examine season-specific survival rates, we generated an overall Kaplan-Meier product-limit cumulative survivorship distribution with PROC LIFETEST (Kaplan and Meier 1958, Pollock et al. 1989, Fox 2001, Winterstein et al. 2000). We modeled the effects of species, period (i.e., 2000–2001 dry vs 2004–2006 wet), and species×period on survival with Cox proportional hazards regression in PROC TPHREG, which we also used to generate predictions by species and year (Fox 2001, Kalbfleisch and Prentice 2002, SAS 2004, Kleinbaum and Klein 2005, Murray 2006). We simplified the rain effect because we felt that prior information was inadequate and our time series not long enough to fully define potentially intricate lagged relationships that may respond quicker to rain than drought. We were unable to model an age effect because we did not have reliable age data from 2000 and 2001 when deer were aged by tooth wear (Erickson et al. 1970, Gilbert and Stolt 1970, Hamlin et al. 2000, Gee et al. 2002, S. Haskell, unpublished data). For AICc comparisons among these semiparametric and partial-likelihood models (Kalbfleisch and Prentice 2002, SAS 2004, Kleinbaum and Klein 2005, Murray et al. 2006), we calculated the number of estimated parameters according to differences between -2×log-likelihood and AIC given by SAS and used a sample size equal to the number of mortality events.

In all Cox regression analyses, we tested the proportional hazards assumption from the preferred model by correlating Schoenfeld residuals with the natural logarithm of event times and extended the Cox model with time-dependent covariates if necessary (Therneau and Grambsch 2000, SAS 2004, Kleinbaum and Klein 2005, Murray 2006); we used PROC CORR for these relationships. We assumed noninformative censorships independent of hazard risk (Kalbfleisch and Prentice 2002, Kleinbaum and Klein 2005), which seemed justifiable given that most censorships occurred later in the study likely due to battery failures in ≥4-year-old collars.

Fawn Capture.— We modeled incidence of fawn gender with logistic regression using PROC LOGISTIC (McCullagh and Nelder 1989, Floyd 2001, SAS 2004). We considered predictor variables of offspring number, ranch location (north vs. south), species, year, relative adult female weight (i.e., individual residual error from the preceding weight model), adult female age, age^2, and species×year. Fawn gender was independent of birth date (Haskell et al. 2008a). We estimated confidence intervals for partial parameters by profile likelihood (SAS 2004). We assessed overdispersion in the global model and need for quasi-likelihood inference with the Pearson chi-square goodness-of-fit statistic (McCullagh and Nelder 1989, Burnham and Anderson 2002). Because we were missing 1 and 3 observations for fawn weight and doe body fat, respectively, we tested the significance of those variables by partial p-values after inclusion in the best model selected by AICc.

We modeled fawn weights with normal theory regression and maximum likelihood estimation using PROC GENMOD (Neter et al. 1996, Gotelli and Ellison 2004, SAS 2004). We considered a similar set of predictor variables as for the gender analysis except that we excluded gender (according to the weight effect in the gender model) and included the age of the fawn at capture to potentially help explain nuisance variance. We log-transformed age at capture to help control the influence of outliers and satisfy the assumption of homoscedasticity (Neter et al. 1996). We used the scaled Pearson chi-square statistic to assess structural goodness-of-fit in the global model (SAS 2004). We examined assumptions in the preferred model by plotting raw residuals against expectations (P. Westfall, EIC *The American Statistician*, personal communication).

Fawn Mortality and Recruitment.— We monitored female-fawn groups intensively by radiotelemetry after fawn capture and omitted fawns from survival analyses if our capture operations appeared to cause separation and early mortality (Haskell et al. 2007). We did not enact a 7-day censorship period following captures because if 1-week survival is naturally low, such a censorship period would cause positively biased survival estimates and undue loss of information (Haskell et al. 2007). We monitored fawns until 365 days-old, right-censored individuals when last heard or when a collar was dropped, and determined an end recruitment period for our study by examining the overall Kaplan-Meier survivorship distribution and latest recorded mortality. We did not use staggered entry or left-censorship because mortalities occurring early in the field season could bias survival estimates negatively and variance estimates positively (Winterstein et al. 2001, Heisey and Patterson 2006, Murray 2006).

We examined potential influences on fawn survival with a marginal Cox model for clustered data in PROC TPHREG because survival of siblings may not be an independent process (Lee et al. 1992, Gaillard et al. 1998*b*, SAS 2004). We accounted for adult female condition by using individual residuals from the best adult weight model. Similarly, we used individual residuals from the best fawn weight model to potentially account for some nuisance variance in survival models. Four fawns of unknown gender died near birth, so we randomly assigned 2 as males and 2 as females to prevent spurious results with this categorical variable. We were missing weight data for 4 fawns from known females, 1 of which was predated prior to capture and 3 of which were discovered as mummified fetuses. Because these observations provided useful information for the larger analysis, we assigned weight residuals equal to 0. Mean birth dates differed between species and among years (Haskell et al. 2008*a*), so we considered absolute deviations from these 6 means.

Judging by univariate relationships, rain during the pre-rut and rut period would likely be a poor predictor of subsequent fawn survival. However, rain during gestation would correlate well with mule deer survival, and rain during late gestation and lactation would correlate well with white-tailed survival. With larger sample sizes and lesser survival in 2004 and 2005, mule deer mortality would have greater power in determining relative significance of rain periods in these partial likelihood models, thus favoring the gestation period (Kalbfleisch and Prentice 2002, Kleinbaum and Klein 2005). This would be a biologically unreasonable and spurious result (Anderson et al. 1972, Carroll and Brown 1977, Millar 1977, Parker et al. 1990, Andersen and Linnell 1998, Ginnett and Young 2000), particularly for this study (see Discussion), so we chose to model rain during the late gestation and lactation period only. After a best model was determined by AICc, we explored the predictive capacities of Palmer indices during the late gestation and lactation period and the statistical significance of adult female body fat.

We described mortality patterns within and among years. Also, to examine the hypothesis that reduced survival during dry periods was due to sickness-starvation rather than predation, we used competing risks Cox regression with a single global model including covariates from the best previous survival model and a species×rain interaction term (Lunn and McNeil 1995, Kleinbaum and Klein 2005, Heisey and Patterson 2006). This method may be more powerful than using cumulative incidence functions and allows greater breadth of inference than modeling each mortality cause separately (Fine and Gray 1999, Andersen et al. 2002, Rosthøj et al. 2004, Kleinbaum and Klein 2005). To examine the 2 primary causes of death, we right-censored the few observations (*n*=4) with cause of death either unknown or other than sickness-starvation and predation. This and other such methods using covariates to model survival probabilities assume independence among competing risks as an extension of the assumption of noninformative censorships (Kalbfleisch and Prentice 2002, Kleinbaum and Klein 2005). There may be no way to test the veracity of this assumption or remediate methods if substantial violation is suspected (Moeschberger and Klein 1995, Kleinbaum and Klein 2005), but if covariates remain time-dependent for both competing risks, dependence between risk types may exist (Kalbfleisch and Prentice 2002). Ancillary information may be used to assess the independent risk assumption (Kalbfleisch and Prentice 2002) that may be invalid if neglected fawns prone to sickness and starvation make themselves more susceptible to predation by seeking their dam or vocalizing (i.e., direct compensatory mortality; Atkeson et al. 1988). Thus, cautious interpretation of modeling results may be warranted.

Thymus Glands and Weaning.—We modeled thymus gland weights similarly as fawn weights, but with a more limited sample, we considered only additive predictor effects of fawn age at death when glands were collected and cause of death. Assuming similar randomness, we pooled observations from predation and other causes to be compared with thymus weights from sick-starve fawns. To reduce influence of outliers, help satisfy the assumption of homoscedasticity, and prevent negative predictions, we log-transformed the response variable (weight) and the predictor variable of fawn age.

We could not use accelerated failure-time regression to model factors affecting weaning times (e.g., Haskell et al. 2008a) because precise weaning dates could not be determined. Thus, we modeled incidence of weaned dead fawns (i.e., no milk in stomach) with logistic regression, similarly as fawn gender, understanding that a time component existed. We did not consider weaned observations for fawns ≤3 days-old, assuming to that to live >3 days, fawns would have been fed at least once. We presented but did not model weaned observations for fawns >60 days-old because fawns may normally be weaned as functional ruminants at that time (Short 1964, Sadleir 1980b, Hirth 1985). We considered potential explanatory variables of species, gender, ranch location, mortality type, rain from May–August, and species×rain. We did not consider potential covariates that would rely on data from adult females because the limited sample size would have been reduced to explain more complex models.

Maternal Antipredator Strategies.— We estimated simultaneous locations within postpartum familial groups by maximum likelihood and weighted-incenter methods depending on which method was predicted to perform better (Haskell and Ballard 2007*b*; S. Haskell, unpublished data). We removed entire group observations from the final data set when predicted linear error for 1 individual observation was >200 m. Predicted linear errors were often correlated within a group observation because of similar triangulation geometries and distances between receiver and transmitters, so realized location errors were probably not random in direction which would diminish the overall effect of error in estimating group cohesion statistics. We used MATLAB to measure Euclidian distances between the estimated locations of adult females and fawns and between twin fawns as the response variables of interest.

To avoid the pitfall of excessive power in detecting spurious effects (Johnson 1999, Anderson et al. 2001), we did not use mixed regression modeling, but instead treated each familial group as an experimental unit, described spatial statistics between species and periods by bootstrapping, and tested research hypotheses with 2-sided randomized t-tests (no. iterations = 3,000; Gotelli and Ellison 2004, Manly 2007). We used multiple observations of a group as a subsample. We divided each subsample between 2 periods: 1) <3 weeks postpartum during the hider phase (Lent 1974), and 2) >30 days postpartum through late winter, as previous research on white-tailed deer indicated that postpartum group cohesion may become tighter around 4 weeks postpartum (Demarais et al. 2000). We tried to obtain at least 11 subsamples per group per period, but mortalities often precluded this goal, so we only used groups with ≥4 subsamples within a period. We used the median of the subsample distances to represent the sample value to reduce effects of outliers caused by factors of disinterest such as adult female excursions to permanent water sources or temporary effects of semi-permeable barriers (e.g., fences, roads, and rim-rock). In the case of group triads (i.e., female with twin fawns), we averaged the simultaneous distances between a female and her 2 fawns to be used as a subsample value for the female-fawn analyses.

We examined kill-sites for evidence of antipredator defense by adult females. There were no fawns killed by predators from 22–34 days-old, but there were 2 fawns killed at 21 and 22 days-old. To maximize sample size, we included these 2 fawns in hider-phase predator mortality analyses. We recorded incidences of predated fawns that were not consumed by the predator as evidence of maternal defense. We used the 2-sided Fisher exact test for comparison of proportions to test differences of carcass consumption rates between species during the hider phase (Zar 1999). Considering the possibility of dependent competing risks, we examined evidence for relative success of maternal defense strategies by presenting proportions of predated fawns <23 days-old by species and year. We did not attempt significance tests of these naïve binomial statistics but relied on qualitative interpretation of 95% confidence intervals (Cherry 1998, Heisey and Patterson 2006). We described 3 other relevant observations.

RESULTS

Adult Female Capture

In February 2000, we captured and fitted 30 females of each species with radiocollars. In February 2001, we captured and collared an additional 10 mule deer and 13 white-tailed deer. In April 2004, we captured 25 females of each species. In April 2005, we recaptured 49 females from the previous year and captured an additional white-tailed female that was a short-yearling, originally captured and collared as a neonate during summer 2004. Also in 2005, 2 white-tailed females broke a front leg during capture operations, so we replaced these deer for the fawn survival study. In April 2006, we recaptured 42 females from the previous year and captured an additional 5 white-tailed deer and 7 mule deer to compensate for mortalities, including 1 mule deer that broke its neck during capture in 2006. Two and 1 white-tailed females may have succumbed to capture myopathy in 2005 and 2006, respectively.

Ages and Reproductive Rates.— Nearly half of the mule deer captured in 2004 were yearlings approaching their second birthday; overall, white-tailed deer tended to be older (Fig. 4). Because we recaptured deer every year, the age structure grew older from 2004–2006 (Fig. 4). In 2004 and 2005 following pre-rut and rut periods of abundant rain

(Fig. 5), all females were pregnant and most with twins, including 2 white-tailed short-yearlings: 1 with a singleton in 2004, and 1 with twins in 2005. One mule deer had triplet males in 2004. Of the 11 mule deer yearlings captured in 2004 (Fig. 4), we field-verified that at least 10 had twins. In 2005, we verified that the mule deer female bred as a 12-year-old also had twins. Because female age appeared irrelevant of fecundity (presumably excluding fawns), we made simple comparisons between species among years (Fig. 6). Reproductive rates for both species appeared lower in 2006 following an autumn period of less than normal rain (Figs. 5, 6). Three females captured in 2006 were not pregnant, including 2 mule deer recaptures and a white-tailed short-yearling.

Overall, productivity was similar between species although consistently greater for mule deer (Fig. 6). In particular, white-tailed fetus counts may have been underestimated by ultrasound in 2006 due to relative inexperience of the user examining many white-tailed deer that year. Assessing general pregnancy status was the priority, and identifying fetal twins was not always straightforward. Also, because mule deer on average birthed 1 month later than white-tailed deer (Haskell et al. 2008a), larger white-tailed twin fetuses may have been more difficult to differentiate (O. Alcumbrac, Wildlife Health Services, personal communication). Of 153 fetal counts (Fig. 6), by subsequent field observations we verified 56 correct counts, including 1 case of triplets, and determined that we had underestimated fetal number 13 times and overestimated 3 times. Overall, productivity appeared similar between 2004 ($\bar{x}$ = 1.90 fawns/female ± 0.10, 2 SE) and 2005 ($\bar{x}$ = 1.84 fawns/female ± 0.10, 2 SE) but lower in 2006 ($\bar{x}$ = 1.58 fawns/female ± 0.17, 2 SE).

Body Weights.— We analyzed weights from 66 females captured in 2004–2006, 37, 13, and 16 of which were captured and weighed 3 successive times, twice, and once, respectively, for a total of 153 observations. From the global model explaining adult deer weights, we removed terms in this order: 1) species×year interaction ($F_{2,91} = 0.28$, $P = 0.755$), 2) location ($F_{1,89} = 1.56$, $P=0.214$), 3) species ($F_{1,64} = 36.38$, $P \leq 0.001$), 4) year ($F_{2,112} = 34.30$, $P \leq 0.001$), 5) age^2 ($F_{1,147} = 15.00$, $P \leq 0.001$), and 6) age ($F_{1,153} = 3.77$, $P = 0.054$).

The model with effects of species, year, and age quadratically was the best model explaining weights of adult females (Tables 2, 3). The 2 species responded to annual effects similarly, and grazing practices (i.e., location effect) had little effect on deer weights after accounting for other factors. Mule deer were heavier than white-tailed deer, and deer were of similar weights in 2004 and 2005 but lighter in 2006 (Fig. 7, Table 3). In comparison to rain patterns (Fig. 5), a mean of the previous pre-rut and rut period and gestation period may best explain deer weights in April (Fig. 7). Deer generally gained weight until 6 years-old, at which time they lost weight with increased age (Fig. 8). By including the age effect in regression models, we controlled the potential nuisance that changing age structure (Fig. 4) may have had on other effects. We verified that compound symmetry was the preferred covariance structure, and residuals appeared normally distributed. A likelihood ratio test against a null model with independent errors concluded that the repeated measures model was preferred ($\chi^2_1 = 80.9$, $P < 0.001$), indicating that relatively heavy or lightweight deer existed.

While body fat and weight were correlated for mule deer ($n = 77$, $r = 0.263$, $P = 0.021$) and white-tailed deer ($n = 73$, $r = 0.379$, $P = 0.001$), we were reluctant to model body fat because those data likely suffered from measurement errors that were biased among various ultrasound users within and among years. Also, we were missing 3 data points for body fat estimates. Body fat estimates appeared similar between species and may have been greater in 2005 (*n* = 50, $\bar{x}$ = 12.1% ± 0.8, 2 SE) than in 2004 (*n* = 50, $\bar{x}$ = 10.8% ± 0.8, 2 SE) and were likely lower in 2006 (*n* = 53, $\bar{x}$ = 8.5% ± 0.4, 2 SE) as were weights.

Blood Parameters.— Blood results from 2004 were negative for BVD and IBR, but all deer tested positive for EHD and BT antibodies. The respiratory diseases of PIV-3 and BRSV were also sero-prevalent in deer, particularly in mule deer (Fig. 9). In 2005, 48 of 51 deer tested positive for either EHD or BT; 41 were positive for both. One of the double-negative deer was a surviving white-tailed short-yearling that was captured as a neonate in summer 2004.

In 2004, 4 white-tailed and 3 mule deer had trace amounts of vitamin E with <0.5 µg/ml in sera. Otherwise, ranges of selenium (*n* = 50), vitamin E (*n* = 40), and vitamin A (*n* = 47) were 0.09–0.32 ppm, 0.5–3.1 µg/ml, and 0.44–2.01 µg/ml, respectively. In 2005, ranges of selenium (*n* = 16) and vitamin E (*n* = 17) were 0.07–0.13 ppm and 0.67–4.20 µg/ml, respectively. In 2004, vitamin A was sufficient ($\bar{x}$ =0.93 µg/ml ±0.10, 2 SE; McDowell 1985). Overall, selenium concentrations were within adequate levels for ruminants (McDowell 1985, Robbins 1993, McDowell et al. 1995), but vitamin E may have been deficient in 2004 (Fig. 10; National Research Council [NRC] 2007, C. Barr, Texas Veterinary Medical Diagnostic Lab, personal communication). Some of the annual differences could have been caused by laboratory analytical methods (Stowe and Herdt 1992, NRC 2007).

Adult Female Survival

We began the survival periods of 1 May 2000, 2001, and 2004–2006 with 30, 39, 29, 26, and 28 mule deer and 30, 36, 38, 28, and 28 white-tailed deer, respectively. In the same respective years we had 1, 3, 8, 0, and 3 censorships. From about 300 deer-years, we recorded 31 mortalities unrelated to our capture operations. Due to scavenging, we were unable to assign cause-of-death in 12 cases, but 12 were sick-starve. Of the 12 known sick-starve deer, 7 were likely >10 years-old. There was 1 predator-kill which was by bobcat. Hunters also harvested 1, and poachers killed 3. Two were killed by automobiles, making road-kill as effective at top-down limitation as predators and hunters combined, with cumulatively negligible influence.

Overall, seasonal periods of reduced survival appeared to be from August–mid-October and mid-November–February, representative of the lactation and weaning period and the rut and post-rut period, respectively (Fig. 11). Survival from March–July was relatively constant (Fig. 11). White-tailed deer survival increased from the drought period in 2000–2002 to the wetter period in 2004–2007, but mule deer survival decreased between the same periods with an apparent lag effect following the rains of 2004 (Figs. 2, 5, 12). Regardless of the drought from November 2005–2006 (Figs. 2, 3, 5), white-tailed survival remained high suggesting carryover effects from previous rains in 2004 and 2005 despite reduced weights and reproduction (Figs. 6, 7, 12).

The model containing effects of species ($\chi^2_1 = 6.23$, $P = 0.013$), period ($\chi^2_1 = 4.61$, $P = 0.032$), and species×period ($\chi^2_1 = 7.48$, $P = 0.006$) was the best model explaining survival rates (Table 4). Estimated annual survival rates during the drought period from May 2000–April 2002 and the wetter period from May 2004–April 2007 were 0.98 (0.96–1, 95% CI) and 0.87 (0.80–0.94, 95% CI) for mule deer and 0.82 (0.73–0.92, 95% CI) and 0.92 (0.87–0.98, 95% CI) for white-tailed deer, respectively. Residuals for species (r = -0.213, P = 0.249) and period (r = 0.223, P = 0.228) were not significantly correlated with timing of mortality events, indicating that the proportional hazards assumption was satisfactory.

Fawn Capture

We captured 39, 39, and 28 mule deer fawns and 13, 20, and 31 white-tailed fawns during summers of 2004–2006, respectively, for a total of 170 fawns. Of those, 145 were from adult females with known data histories, and 25 were captured from unknown females. On average, living fawns from known females were younger (median = 0.75 days-old, range = 0.05–9 days-old) and weighed less (median = 2.78 kg, range = 0.96–4.88 kg) at capture than fawns from unknown females (median = 6 days-old, range = 0.1–30 days-old; median = 3.77 kg, range = 2.27–7.26 kg). At capture, 112 of the fawns from known females were <1 day-old, 20 were 1–2 days-old, and 13 were >2 days-old.

Fawn Gender.— We could not determine gender of 5 fawns. Overall, sex ratio was skewed with 93 males (56%) and 72 females (z = 1.63, P = 0.102). Of the 165 fawns with determinable gender, 140 (78 males, 62 females) were from known adult females. The global model explaining gender occurrence was not overdispersed ($\chi^2_{79} = 79.99$, P = 0.448; Lindsey 1999), so we did not adjust variance. From the global model, we removed terms in this order: 1) species×year ($\chi^2_2 = 0.603$, P = 0.740), 2) adult female age^2 ($\chi^2_1 = 0.004$, P = 0.952), 3) year ($\chi^2_2 = 0.350$, P=0.840), 4) adult female age ($\chi^2_1 =$ 0.228, P = 0.633), 5) species ($\chi^2_1 = 0.305$, P = 0.581), 6) adult female weight ($\chi^2_1 =$

1.106, $P = 0.293$), 7) location ($\chi^2_1 = 3.899$, $P = 0.048$), and 8) number of offspring ($\chi^2_1 = 4.643$, $P = 0.031$).

The model with number of offspring and ranch location as covariates was the best model explaining occurrence of fawn gender (Table 5). The partial parameter odds ratios indicated greater probabilities of males with increased number of siblings (1.088–8.734, 95% CI) and on the southern more overgrazed ranches (0.228–0.985, 95% CI; with south as reference). Six of 17 (35%) singletons were male, 69 of 120 (58%) twins were male, and all 3 of a triplet set were male. Fifty-four of 105 fawns (51%) on the north ranches and 39 of 60 fawns (65%) on the south ranches were male. When included singly into the best model (Table 5), partial parameters of fawn weight ($\chi^2_1 = 1.788$, $P = 0.181$) and adult female body fat ($\chi^2_1 = 0.618$, $P = 0.432$) were insignificant.

Fawn Weights.— We excluded the same 5 fawns as in the preceding analysis and 1 fawn with no weight recorded. Of the 164 fawns with known weights, 139 were from adult females with data histories. The global model appeared structurally sound ($\chi^2_{127} = 139$, $P = 0.220$). From the global model, we removed terms in this order: 1) species×year ($\chi^2_2 = 1.73$, $P = 0.420$), 2) location ($\chi^2_1 = 1.41$, $P = 0.236$), 3) adult female age^2 ($\chi^2_1 = 1.47$, $P = 0.225$), 4) adult female age ($\chi^2_1 = 3.38$, $P = 0.065$), 5) year ($\chi^2_2 = 4.06$, $P = 0.131$), 6) relative adult female weight ($\chi^2_1 = 5.17$, $P = 0.023$), 7) species ($\chi^2_1 = 11.60$, $P = 0.001$), 8) number of offspring ($\chi^2_1 = 7.87$, $P = 0.005$), and 9) the natural logarithm of fawn age at capture ($\chi^2_1 = 15.71$, $P < 0.001$).

The preferred model excluded the effects of location, species×year, and the quadratic form of adult female age (Table 6). After controlling for a fawn age effect, fawn weights decreased with increasing number of offspring and adult female age (Table

7). Relatively heavy adult females produced heavy fawns, and similar to adult females (Table 3), mule deer fawns were heavier than white-tailed fawns (Table 7). Contrary to adults (Fig. 7), least squares mean differences from the preferred model (Tables 6, 7) indicated that fawns weighed less in 2004 than in 2005 (0.30 kg ± 0.24, 2 SE; $\chi^2_1 = 6.01$, $P = 0.014$). The model suggested that fawn weights then dropped about 0.1 kg from 2005–2006 (Table 7). The fawn age effect suggested that over a 1-week period, fawns gained about 0.06 kg/day (Table 7). When added to the preferred model, adult female body fat was a poor predictor of fawn weight ($\chi^2_1 = 1.14$, $P = 0.285$) while other covariates maintained partial significance. The residual plot suggested that assumptions of constant variance and normality were satisfactory. We did not explore a fawn-age-at-capture×year interaction term to see if growth rates differed among years because the best models excluded fawns from unknown females, thus restricting the analysis primarily to fawns <1 day-old.

Fawn Mortality and Recruitment

We omitted 6 fawns from survival analyses. One fawn was aborted in April 2004 perhaps due to adult-capture stress, and we likely caused permanent separation between adult females and 1 white-tailed fawn in 2005 and 2 mule deer fawns in both 2005 and 2006. Of the 5 latter instances, in 4 cases it was the fawn that distanced itself from its dam and not vice-versa (Haskell et al. 2007). The cumulative survivorship curve asymptoted near 210 days postpartum, and the latest recorded mortality event was by bobcat at 282 days (Fig. 13). Of the 164 fawns sampled, 31 were known to survive 1 year postpartum, and there were an additional 11 fawns right-censored from 285–365 days-old (Fig. 13). Therefore, we ended the study and considered the recruitment period lasting until 285 days postpartum. Thirteen fawns were right-censored before 285 days-old (Fig. 13).

Proportional Hazards.— Fawn survival for both species declined from 2004–2006 cohorts (Fig. 14). The best survival models included covariates relating to known adult females (Table 8), so we excluded fawns from unknown females in all models. Of the remaining 139 fawns, there were 98 mortality events and 41 right-censorships, 10 of which occurred before recruitment. Residuals from the best model explaining fawn survival by AICc suggested that the proportional hazards assumption did not hold for 2 covariates (Fig. 15). Inspection of the time-dependent covariates with heaviside functions (Kleinbaum and Klein 2005) indicated that relative fawn weight was more important near birth and fawn gender was important after 30 days. These were biologically reasonable results, so we extended the Cox model. The fawn weight effect may have been more continuous than the gender effect which may have involved deer behavior (Fig. 15), so for time-dependence we related fawn weight to the natural logarithm of event time and treated gender as a heaviside function with effects before and after 30 days-old (Therneau and Grambsch 2000, Kleinbaum and Klein 2005).

From the global model including the 2 time-dependent covariates, we removed terms in this order: 1) species×rain ($\chi^2_1 = 1.03$, $P = 0.311$), 2) fawn gender <30 days-old ($\chi^2_1 = 0.12$, $P = 0.734$), 3) relative adult female weight ($\chi^2_1 = 0.82$, $P = 0.366$), 4) species ($\chi^2_1 = 0.71$, $P = 0.399$), 5) adult female age^2 ($\chi^2_1 = 0.82$, $P = 0.364$), 6) number of offspring ($\chi^2_1 = 1.52$, $P = 0.218$), 7) adult female age ($\chi^2_1 = 1.19$, $P = 0.276$), 8) location ($\chi^2_1 = 1.83$, $P = 0.176$), 9) total May–August rain ($\chi^2_1 = 9.65$, $P = 0.002$), 10) ln(time)×relative fawn weight ($\chi^2_1 = 9.91$, $P = 0.002$), 11) relative fawn weight ($\chi^2_1 =$

2.43, $P = 0.119$), 12) fawn gender ≥30 days-old ($\chi^2_1 = 10.54$, $P = 0.001$), and 13) absolute deviation from mean birth dates ($\chi^2_1 = 9.23$, $P = 0.002$).

After including the time-dependent covariates, the best model by AICc was the same as before, except for the addition of the parameter relating fawn weight to time and the limitation of a gender effect to ≥30 days postpartum (Table 9); AICc improved by 20.5 indicating a substantially better fit over the similar time-independent model. Increased deviation from mean birth dates increased hazard, and after 30 days-old it became risky to be male (Fig. 15; Tables 9, 10). Increased rain from May–August and increased fawn weights measured at capture both reduced hazards, but the benefit of weight decreased with time (Table 10). Included into the best model (Table 10), adult female body fat was a poor predictor of fawn survival ($\chi^2_1 = 1.23$, $P = 0.267$). Palmer indices of PDSI ($\chi^2_1 = 4.94$, $P = 0.026$) and ZNDX ($\chi^2_1 = 7.97$, $P = 0.005$) were both significant as partial parameters when replacing rain in the preferred model (Table 10), but the indices increased AICc by 5.3 and 2.2, respectively. With less of a lag response, ZNDX performed better than PDSI, but the rain measure was preferred.

Mortality Patterns.— Of the 139 fawns captured from known females and included in survival analyses, 12 (9%) died within 25 m of the birth site; 3 of those were undeveloped fetuses with healthy siblings. Kaplan-Meier product-limit survivorship for the 139 fawns was 91%, 86%, and 78% at 1, 3, and 6 days postpartum, respectively. There were 47 mortalities by sickness-starvation, 47 by predation, 1 by other cause, and 3 undeterminable. The other cause was trauma by intraspecific adult female. Most predation was by bobcat with at least 2 by fox, 1 by great-horned owl, and 1 by turkey vultures as evidenced by frothy blood in the fawn’s mouth and nose. Overall, bobcats took about 31% of the fawn crop. There were no incidences of twin fawns being killed simultaneously. Causes of sickness were various (Appendix A). It seemed erroneous to label incidences of starvation as abandonment (natural or other) because radiotelemetry data indicated that adult females remained near starved fawns before death. Most mortality by predation and sickness-starvation occurred within 45 days postpartum and mainly within 15 days postpartum (Fig. 16). The only 3 mortalities >210 days postpartum were by bobcat (Fig. 16). In 2004 and 2005, mule deer fawns were primarily afflicted by sickness-starvation whereas white-tailed fawns succumbed mostly to predation (Fig. 17). However, in 2006 predation rates increased for mule deer and sickness-starvation was more prevalent in white-tailed fawns (Fig. 17).

From the global competing risks model, we removed terms in this order (mortality type given by capital letters in parentheses): 1) species×rain (P; $\chi^2_1 = 0.17$, $P = 0.682$), 2) time-dependent fawn weight (P; $\chi^2_1 = 0.03$, $P = 0.854$), 3) species (P; $\chi^2_1 = 1.14$, $P = 0.285$), 4) species×rain (SS; $\chi^2_1 = 0.88$, $P = 0.348$), 5) fawn weight (P; $\chi^2_1 = 1.24$, $P = 0.265$), 6) rain (SS; $\chi^2_1 = 3.90$, $P = 0.048$), 7) deviation from mean birth date (SS; $\chi^2_1 = 3.84$, $P = 0.050$), 8) species (SS; $\chi^2_1 = 6.34$, $P = 0.012$), 9) rain (P; $\chi^2_1 = 5.44$, $P = 0.020$), 10) deviation from mean birth date (P; $\chi^2_1 = 6.75$, $P = 0.009$), 11) gender >30 days-old (SS; $\chi^2_1 = 6.33$, $P = 0.012$), 12) gender >30 days-old (P; $\chi^2_1 = 2.88$, $P = 0.089$), 13) time-dependent fawn weight (SS; $\chi^2_1 = 28.60$, $P<0.001$), and 14) fawn weight (SS; $\chi^2_1 = 0.06$, $P=0.811$).

The best model contained most effects for sickness-starvation but fewer for predation (Tables 11, 12). Overall, mule deer fawns succumbed to sickness-starvation more than white-tailed fawns, and no difference was detected for predation with relatively low power in white-tailed fawn samples in 2004 and 2005 (Fig. 17; Tables 11, 12). Mortality rates of both causes appeared to increase with decreasing rain (Figs. 5, 17; Table 12). Given the nature of decreasing rain in May–August from 2004–2006 (Fig. 5), our sample was not powerful enough to detect a difference in slopes of sickness-starvation mortality rates between species from 2004–2006 (Fig. 17, Table 11). Time-dependent fawn weight was important for sickness-starvation but not predation, and deviation from mean birth date was important for both (Tables 11, 12). Fawn weight was a poor predictor of mortality by sickness-starvation without the time-dependent component (see above, Table 11), and gender ≥30 days-old was not a good predictor for either cause without the presence of the same covariate for the other cause, suggesting interaction between competing mortality agents.

Confounding influence of dependence in competing risks may be seen by describing the ≥30 days-old gender effect. In the preferred model (Table 12), the effect appeared stronger for predation. However, 13 of 23 (57%) fawns predated at ≥30 days-old were male, which may be expected given skewed sex ratios at birth and no gender effect <30 days-old, but all 16 (100%) fawns ≥30 days-old succumbing to sickness-starvation were male. Twelve (75%) of those sick-starve events occurred at 30–90 days-old. Ultimately, despite the male bias in neonatal sex ratios, 11 of 31 (35%) recruited fawns were male, which seemed to account for the 1:2.5 adult male:female ratios observed (Haskell et al. 2008*b*).

Based on parameter estimates in the 2 fawn hazard models (Tables 10, 12) and examination of the raw data, we concluded that the other effects in the preferred competing risks model appeared valid. For both species, incidence of predation appeared to increase with reduced rain in May–August from 2004–2006 (Figs. 5, 17; Table 12). This may be explained by reduced hiding cover, but the possibility of interaction among competing risks and direct compensatory mortality cannot be discounted. However, even in 2006, weight residuals of predated fawns were greater than those succumbing to sickness-starvation (Fig. 18), which supports the lack of a fawn weight effect explaining mortality by predation (Table 12). We will address and discuss the issue of interacting risks with additional lines of evidence.

To examine the postpartum behavioral carrying capacity hypothesis in more detail, we added adult female age, quadratically at first, into the preferred competing risks model (Tables 1, 12). We removed terms in this order: 1) age^2 (P; $\chi^2_1 = 0.05$, $P = 0.815$), 2) age (P; $\chi^2_1 = 0.14$, $P = 0.708$), 3) age^2 (SS; $\chi^2_1 = 1.07$, $P = 0.302$), and age (SS; $\chi^2_1 = 3.23$, $P = 0.072$), while other partial parameters maintained greater significance. The adult female age effect for sickness-starvation was borderline significant at the standard $\alpha = 0.05$ level, but colinearity was apparent with the rain covariate, as our sample aged with reduced rain during the late gestation and lactation periods (Figs. 4, 5). In fact, the age coefficient estimate (0.989–1.303, 95% CI) suggested increased hazard with increased age, which was a biologically spurious result opposite of the predicted effect and understandable in light of the colinearity.

Thymus Glands and Weaning.— We sampled 24 fawns for thymus glands. Mean thymus weight was 0.925 g (1.103 SD, range = 0.050–4.721 g, median = 0.440 g). Mean fawn age was 16.8 days-old (22.1 SD, range = 1.5–75 days-old, median = 7.25 days-old). There were 17, 5, and 2 thymus glands from fawns succumbing to sickness-starvation, predation, and other causes, respectively. The 2 observations from other causes were not included in previous survival analyses and were due to trauma by intraspecific adult female (again mule deer) and automobile collision. All predation-related thymus glands were from mule deer, and only 1 was in 2006 because mule deer fawns were consumed more frequently that year (see below). We expended less effort collecting thymus glands in 2004. The model including effects of mortality type and the natural logarithm of age had lower AICc by 0.99 and 5.38 compared to the age and intercept-only models, respectively. Controlling for growth of thymus glands as neonates aged, fawns succumbing to causes of death other than sickness-starvation had heavier glands (Table 13). For the median-aged fawn of 7 days-old, the model predicted that fawns succumbing to sickness-starvation and other causes had thymus glands weighing 0.395 g and 0.894 g, respectively (Table 13). Our thymus glands were smaller than "extremely small" (Ozoga and Verme 1978:794).

We determined stomach contents of 37 dead fawns, 10 of which were >60 days-old and excluded from the regression analysis (Appendix B). The oldest fawn discovered with milk in its stomach was 40 days-old (Appendix B). We failed to achieve maximum likelihood convergence in the global regression model, so we described results qualitatively. The problem with modeling was that all but 1 incidence of weaning from 3–60 days-old was explained by ranch location with premature weaning associated with the southern more overgrazed cattle-only ranch (Appendix B). The same but opposite effect was true for nursed fawns dying ≤40 days-old (Appendix B), suggesting that it was disease and not starvation that afflicted fawns on the northern ranch where grazing was less intense but sheep were present. Most of the fawns known to be nursing and dead were mule deer. Of the 4 nursing white-tailed fawns, 2 were twins in 2006, 1 was predated, and the other was from a 12 year-old female. After the normal 60 day-old weaning period, weaning appeared unrelated to ranch location (Appendix B). Eight of 12 (67%) fawns prematurely weaned were male, supporting the gender effect for sickness-starvation (Appendix B, Table 12). Two of the prematurely weaned fawns were taken by predators (Appendix B), suggesting that starvation and predation may not have been completely independent; despite more general results from thymus glands and fawn weights (Fig. 18), some predation may have been directly compensatory.

Maternal Antipredator Strategies

During the periods of interest, we censored 104 observations and retained 1,804 simultaneous familial deer locations by radiotelemetry and 102 locations by GPS. Mean absolute bearing error by beacon study was 2.3° (Haskell and Ballard 2007*b*), and mean predicted linear error for our location data was 72 m. Mean subsample size for familial groups within periods was 10 locations. Because an inter-annual effect was not anticipated, nearly all data were collected in 2004 and 2005 with data collection in 2006 designed to augment white-tailed samples only. For adult female-fawn analyses, we obtained 26 and 18 samples for mule deer and 21 and 15 samples for white-tailed deer in periods 1 and 2, respectively. For twin fawn analyses, we obtained 16 and 4 samples for mule deer and 7 and 4 samples for white-tailed deer in periods 1 and 2, respectively. During the hider phase (i.e., period 1), mule deer females kept fawns closer together and closer to themselves than did white-tailed females (Fig. 19). After 30 days postpartum, group cohesion was tight for both species (Fig. 19). Although we did not quantify the transition period directly, we did notice white-tailed fawns associating more closely with their dams starting around 4 weeks-old.

During the hider phase, 8 of 13 (62%) predated mule deer fawns and 11 of 11 (100%) predated white-tailed fawns were either dismembered and cached or consumed prior to our discovery ($P = 0.041$). Of the 13 predated mule deer fawns, only 2 of 6 (33%) were consumed in 2004 and 2005 when group cohesion spatial data were collected, whereas 6 of 7 (86%) were consumed in 2006 when adult females were in poorest condition (Figs. 6, 7, 12). Considering the same 139 fawns as in previous survival analyses, 6 of 59 (10%, 5–21% 95% CI) mule deer fawns <23 days-old were predated in 2004 and 2005, and 5 of 27 (19%, 9–38% 95% CI) white-tailed fawns were similarly predated. In 2006, 7 of 25 (28%, 15–49% 95% CI) mule deer fawns <23 days-old were predated, and 6 of 28 (21%, 11–41% 95% CI) white-tailed fawns were similarly predated. Predation rates of white-tailed fawns during the hider phase appeared consistent among years, whereas the predation rate of mule deer fawns appeared initially lower than that of white-tailed fawns but rose in 2006 when adult females were in poorest condition.

In 2004, we recovered a 41-day-old mule deer after it was motionless for 16 hrs as determined by the radiocollar PET; the fawn was alive but unresponsive with fatal wounds from a bobcat to trachea and lungs; as in many cases of predated mule deer fawns, there were adult hoof prints stomped into the hard soils. In 2005, we recovered a 7-day-old mule deer after it succumbed to an infection in its belly from a wound delivered by a bobcat, indicating that it survived the initial attack. Also in 2005, while inspecting the kill-site of a 3-day-old mule deer that was consumed by the predator, 15 m from the site we found a gray fox that was stomped to death by an adult deer.

DISCUSSION

There has been contention over removing teeth to age ungulates (Festa-Bianchet et al. 2002, Nelson 2002), but aging by cementum annuli remains the only method considered precise and accurate after deer are ≥2 years-old (Erickson et al. 1970; Gilbert and Stolt 1970; Hamlin et al. 2000; Van Deelen et al. 2000; Gee et al. 2002; S. Haskell, unpublished data). As a recessed canine likely useful for resource competition in the early stages of deer evolution (Geist 1998), removal of the I4 tooth probably has negligible effect on physiological performance and foraging efficiency of deer as selective feeders (Kay 1987, Hirth 2000, Nelson 2001, Bleich et al. 2003), but absolute certainty is impossible. Animal age may or may not be an important consideration when modeling natural processes (Mech and McRoberts 1990*a*, 1990*b*; Nelson and Mech 1990; DelGiudice et al. 2006, 2007; Haskell et al. 2008*a*), but if so, accurate estimates are desirable (Leberg et al. 1989). Whether animal age is a covariate representing a research hypothesis or is an uninteresting factor that may likely explain some nuisance variance in the response, researchers must obtain reliable estimates to facilitate discovery of truth. Particularly for data like ours in which there appeared to be a net-gun capture bias for yearling mule deer in 2004 and an aging sample of recaptured deer in 2005 and 2006 (Fig. 4; also see Anderson et al. 1974), undesirable and potentially masking age effects should be controlled by inclusion as a predictor variable in regression modeling when biologically appropriate.

We could not include age as a covariate explaining adult female survival (e.g., Nelson and Mech 1990, Garrott et al. 2003, DelGiudice et al. 2006) because of limitations of data from 2000 and 2001, but mortalities were few, so power to detect an age effect would have been low after considering species, period, and the interaction thereof. Based on evolution and comparative ecology, we expected that adult white-tailed survival would be lower than that of desert mule deer during the drought period and would increase with rain (Figs. 2, 3, 12; Tables 1, 4). However, we did not expect mule deer survival to decrease after the phenomenal rains of 2004 (Figs. 2, 12). Half of the mule deer mortality in 2005 was explained by poaching, and another deer that died was 12 years-old, so natural mortality in 2005 did not seem reduced. The same cannot be said for 2006. Of the 28 mule deer beginning the May 2006–2007 survival period, only 1 was poached, and 5 succumbed to sickness-starvation. These latter deer were near prime-aged (Fig. 8), as 2, 1, and 2 were 4, 6, and 9 years-old, respectively. While adult white-tailed survival responded quickly and positively to increased rain, mule deer survival appeared to exhibit a more lagged and negative response to increased rain. Despite the dry period from autumn 2005 through 2006 (Figs. 3, 5), high white-tailed survival lagged through time (Fig. 12). Adult female survival tends to be the least variable vital rate in ungulate populations, so observed variability in this parameter may be clear indication of physiological stress near some ecological carrying capacity (Gaillard et al. 2000).

Although our sample of old deer was limited (Fig. 12), our data were consistent with other findings that free-ranging deer did not experience reproductive senescence (Teer et al. 1965, Nelson and Mech 1990, Garrott et al. 2003, DelGiudice et al. 2007). Productivity remained high for both species but did appear to decrease in 2006 following the dry pre-rut and rut period of 2005 (Figs. 5, 6). We did not predict variable productivity among years, but in hindsight, as carrying capacity responded to rain it created a situation analogous to the density-dependent productivity reported for a deer herd in central Texas (Teer et al. 1965). In 2004 and 2005, pregnancy rates were 100% and fetal rates were higher than those (1.23–1.72 fetuses/female) reported elsewhere for free-ranging deer (Fig. 6; Teer et al. 1965, Barron and Harwell 1973, Salwasser et al. 1978, McCullough 1979, Andelt et al. 2004), but similar to those by DelGiudice et al. (2007). Unlike other studies (Robinette and Gashwiler 1950, Teer et al. 1965, Robinette et al. 1973, McCullough 1979, DelGiudice et al. 2007), yearlings were as fecund as older deer, but most yearlings were in 2004 following the wet pre-rut and rut period of 2003 (Figs. 4, 5). With a relatively high density of deer at our site (approx 30 deer/km^2) and an adult male:female ratio of 1:2.5 (Haskell et al. 2008*b*), it seems likely that all females achieving estrus were bred. Because the energetic cost of gestation is low compared to cost of lactation, it is an evolutionarily advantageous strategy for females, even in poor condition, to conceive with a chance of favorable environmental conditions at parturition (Murphy and Coates 1966, Millar 1977, Loudon 1985, Carl and Robbins 1988, Parker et al. 1990).

Our data were consistent with other findings that female deer reached maximum size at 5–8 years-old at which time they declined (Fig. 8; Teer et al. 1965, Mech and McRoberts 1990*a*), but this may not be true in all cases (Anderson et al. 1974). Similar to reproductive data, the best model explaining adult female weights indicated reduced weights for both species following the dry period from autumn 2005 through spring 2006 (Figs. 3, 6, 7; Tables 2, 3). While it seems plausible for the white-tailed deer, we question that it was this acute dry period that caused similar negative responses in mule deer weights and productivity. Following a period of prolonged drought in the mid–late 1990s which continued through 2002 (Fig. 3; Lawrence et al. 2004), mule deer survival was high (Fig. 12), making it difficult to reason that a brief dry period would negatively influence mule deer survival while white-tailed deer survival remained high (Fig. 12, Table 4). Also, the 2 adult females found barren in April 2006 died later that year, suggesting not only that they were in dire circumstances but that their problems began before breeding and the onset of the dry period in late 2005 (Fig. 5).

We believe that fawn mortality data will lend credence to our post hoc hypothesis that mule deer weights, productivity, and survival decreased in 2006 because of the substantial rains of 2004 and 2005 that likely benefited the *Culicoides* (biting midge) vector of *Orbivirus* and other bacterial or viral pathogens. *Orbivirus* antibodies were chronic and ubiquitous in sera tests but did not appear heterospecific. Most parainfluenza and bovine respiratory syncytial virus infections tend to be repeated and subclinical, but PIV-3 can be particularly deadly (Van Campen and Early 2001); these respiratory diseases appeared more common in mule deer (Fig. 9). Without a longer time series it is impossible to know the environmental intricacies that drive these populations; adult weights and productivity and fawn survivorship during extended drought are the missing data.

Fawn Mortality and Recruitment

Other researchers found stillborn neonates while catching fawns with unknown birth sites (Ricca et al. 2002, Pojar and Bowden 2004). We only found stillborns when we located birth sites, and 9% of 139 fawns died <25 m from birth sites, suggesting that other areas may also have high rates of neonatal mortality that go undetected unless fawns are captured from birth sites (Murphy and Coates 1966, Verme 1977, Linnell et al. 1995, Andersen and Linnell 1998, Andelt et al. 2004). The fawns we captured from unknown females were a median age of 6 days-old, at which time overall survivorship was 78%. From our observations, we believe that the critical neonatal period (Lent 1974) is about 0.5–2 hrs postpartum and that risk of marking-induced abandonment is negligible (Carstenen Powell et al. 2005, Bishop et al. 2007, Haskell et al. 2007). Therefore, arbitrary post-capture acclimation periods are not appropriate for fawn mortality studies, and abandonment should be determined by radiotelemetry (Haskell et al. 2007).

Overall, mule deer fawns succumbed to sickness-starvation more than did white-tailed fawns (Table 12, Fig. 17). After the rains of 2004, mortality rate of sickness-starvation increased by almost 20% for mule deer fawns in 2005 (Fig. 17). Despite relatively high predation rate for white-tailed fawns in 2005, overall mule deer survival was significantly lower that year (Figs. 14, 17). In general, bobcats as the primary predator killed relatively healthy fawns (Fig. 18, Table 13), but evidence for some direct compensatory mortality of unthrifty fawns included: 1) a time-dependent covariate for both competing risks in the best Lunn-McNeil model (Table 12), 2) predation of 2 fawns <16 days-old known to be prematurely weaned (Appendix B), and 3) greater rates of mule deer fawn carcass consumption in 2006 when adult females were in poorest condition. Thus, while decreased survival of white-tailed fawns in 2006 was mostly due to increased sickness-starvation during the dry period, the reduced rate of sickness-starvation and increased rate of predation for mule deer fawns in 2006 may have indicated some interaction between competing risks (Figs. 5, 14, 17).

With negligible top-down limitation on the adult portions of these sympatric deer populations, predator and sick-starve related fawn mortality appears to be the only factor preventing population eruption and severe malnutrition in adults (Teer et al. 1965, Carroll and Brown 1977, Dickinson et al. 1980, Cook 1984). In particular, bobcats can be expected to cull as much as 31% of fawns even during the best rain-years. Despite the fact that they generally kill healthy fawns, making mortality directly additive, in a long-term context bobcat predation may be to some degree compensatory by mitigating negative density-dependent responses to a fluctuating environment.

Disease usually seems to play a minor role in fawn mortality, and when identified, it has most often been bacterial and not viral (Cook et al. 1971, Carroll and Brown 1977, Wood et al. 1989, Linnell et al. 1995). Pathogens afflicting fawns appeared various, and many were symptomatic of viruses, including the orbiviruses chronic in adults (Appendix A). Most white-tailed fawns succumbing to sickness-starvation appeared to starve, but most mule deer fawns succumbing to sickness-starvation were diseased (Appendices A, B; S. Haskell, personal observation). The weaning data suggested that starvation was important on the more overgrazed cattle-only southern ranches, and disease was important on the less overgrazed sheep-and-cattle northern ranches (Appendix B).

The best Lunn-McNeil competing risks model (Table 12) contained only 1 individualistic parameter for predation, and that was related to fawn birth date; the gender effect seemed spurious, perhaps the result of dependent competing risks. Predation rate did increase with reduced rain (Fig. 17, Table 12), but as previously discussed, this may have been somewhat compensatory, particularly for mule deer. In contrast, risk of sickness-starvation was a function of time-dependent relative fawn weight and gender as well as birth date (Table 12). It is important to note that we used individual residuals from the fawn weight model (Table 7) to model fawn survival. While others found that heavier fawns survived better (Verme 1963, 1977; Nelson and Woolf 1987; Raganelia-Pelliccioni et al. 2006), fawn survival was greatest in 2004 when fawns weighed least (Fig. 14, Table 7); substantial rain and improved range condition during late gestation and lactation outweighed the potential negative influence of drought prior to conception (Figs. 2, 3, 5). After about 30 days-old, males that were more prevalent on the southern more overgrazed ranches were at greater risk of sickness-starvation (Fig. 15; Tables 5, 12; see Results), and premature weaning data indicated that it may have been due to starvation in particular (Appendix B).

The adaptive nature of synchronized birthing has been recognized in terms of seasonality of resources and predator swamping (Begerud 1974, Rutberg 1987, Whittaker and Lindzey 1999, Sinclair et al. 2000, Post et al. 2003). Absolute deviation from mean birth date by species and year was associated with increased hazard of predation and sickness-starvation (Table 12). Although post hoc (Table 1), this result supported the predator swamping hypothesis. Because of the benign transition from winter to spring at our site and the concentration of mortalities near birth (Fig. 16), the birth date effect for sickness-starvation required a more individualistic explanation beyond evolution in response to a seasonal environment. The oldest females were among the earliest to birth (Haskell et al. 2008*a*), and their fawns were stillborn or typically did not survive long. Similarly, primiparous females, particularly those that were bred as fawns, birthed late to relatively unfit fawns. Regardless of cause, if early-born fawns are likely to die while samples are small, the staggered entry approach to survival analysis should not be used (Winterstein et al. 2001, Heisey and Patterson 2006, Murray 2006).

Birth-date data from this study supported the hypothesis that intraspecific social dominance behavior affected the breeding biology of both species (Ozoga and Verme 1986*a*,*b*; Nixon and Etter 1995; Haskell et al. 2008*a*). However, we found no direct support for the postpartum behavioral carrying capacity hypothesis (Table 1) after incorporating other covariates in the fawn survival and competing risks models such as adult female weight, deviation from mean birth date, and relative fawn weight. Studies of red deer (*Cervus elaphus*), zebras (*Equus zebra zebra*), and Cuvier's gazelles (*Gazella cuvieri*) documented greater rearing success of socially dominant females (Clutton-Brock et al. 1982, 1986; Lloyd and Rasa 1989; Alados and Escos 1992), but female condition may not be discounted. Previous social interactions may supersede the effect of body weight in determining social hierarchy among deer (Taillon and Côté 2006). Therefore, deer age can be an independent determinant of dominance rank relative to body weight. The influence of dominance rank on reproductive success of ungulates can be expected to vary both interspecifically according to life history traits and intraspecifically by ecological context (Ellis 1995). At relatively high densities with low resource availability, such as in our study, social behavior may be more tolerant of scramble competition (Michael 1964, Krämer 1973, Betrand et al. 1996, Bowyer et al. 1998, Koenig 2000).

Fawn weaning and weight-at-death data were problematic in that it was difficult to get these data reliably from predated fawns that would have provided information for a relatively healthy sub-sample of the fawn population. Results from captive studies may not be expected to be representative of free-ranging populations, but they can sometimes provide useful baseline information (Haskell et al. 2007). Weight gain and weaning in fawns has been described almost exclusively from captive animals. Until about 3.5 months-old, twin white-tailed fawns gained an average of about 0.28 kg/day (Verme 1989). Other captive studies demonstrated fawn weight gain of 0.21–0.29 kg/day on variable diets (Verme 1963, Murphy and Coates 1966, Robinette et al. 1973, Thompson et al. 1973, Robbins and Moen 1975). For well-fed fawns, growth rates may be more rapid <2 weeks-old than later (Cowan and Wood 1955, Robinette et al. 1973), but for malnourished fawns, weight gain may increase when >15 kg as the fawn becomes less reliant on its dam (Robbins and Moen 1975). Holding other parameters in the fawn weight model constant (Table 7), captured fawns were just representative of the first week postpartum, and predicted weight gain was a meager 0.06 kg/day. Examination of intact carcasses yielded a more long-term prediction of 0.11 kg/day (Fig. 20). Two 1-month-old mule deer nearly achieved weight gain similar to captive fawns before succumbing to an acute hemorrhaging disease (Appendix A photos 13; Fig. 20). Our model was in concordance with others finding that heavy females produced heavy fawns and singletons were heaviest (Table 7; Verme 1963, Sadleir 1980*a*).

For captive deer, peak milk production was about 10–37 days postpartum, and complete weaning was observed from 84–238 days postpartum (Sadleir 1980*b*). Fawns chewed solids at 1 week-old, but forage intake was not appreciable until 25 days-old (Sadleir 1980*a*). Fawns weighing 15 kg increased forage intake and had stomach sizes and contents of similar proportion as adults at about 25 kg or 4 months-old (Short 1964, Robbins and Moen 1975). By 90 days-old, >80% of fawns’ digestible energy was from solids (Sadleir 1980*a*). Nursing has been observed 4 months after the peak of fawning (Bowyer 1991), but milk curds were about 5% of stomach contents by 2 months-old and nearly absent in 3 month-olds (Short 1964). With reduced growth rates at our site, complete weaning should be later (Millar 1977). However, the oldest fawn that we found with milk in its stomach was just 40 days-old (Appendix B).

Fawn weight and weaning data were consistent with the hypothesis that female deer invested relatively little energy into fawn rearing (Table 1; Haskell et al. 2008*a*). Fawn gender and weaning data were suggestive that females on the more overgrazed ranches produced predominantly males because males typically disperse from the home-range more than females (Hawkins and Klimstra 1970, Verme 1983, Nelson and Mech 1984, Caley and Nudds 1987, Aycrigg and Porter 1997), even though adult females on the more overgrazed southern ranches did not weigh less (Tables 2, 3).

Short-term environmental variables associated with the period of late gestation and lactation can be useful to predict fawn survival in more southern temperate regions (Ginnett and Young 2000, this study), but longer-term environmental indices may be appropriate in more northern regions (Picton 1984, Haskell and Ballard 2004). However, the latter studies could not account for variability in reproductive rates associated with weather from the year prior to birthing that may or may not have an effect depending on specific population ecology (Garrott et al. 2003). In west-central Texas, recruitment appeared to be a function of reproduction and fawn survival rates that were affected by rain prior to conception and during late gestation and lactation, respectively (Figs. 3, 5, 6, 14). However, the underlying proximate influences may differ between white-tailed deer that appeared more susceptible to drought and mule deer that may have been more susceptible to pathogens and the associated lag effects of wet weather.

Maternal Antipredator Strategies

Mule deer adults tend to be more aggressive than white-tailed deer against predators such as coyotes (Lingle 2001, Lingle and Pellis 2002). Mule and black-tailed deer are known to actively and successfully defend their fawns from coyotes (Dasmann and Taber 1956, Hamlin and Schweitzer 1979, Truett 1979, Wenger 1981). During flight behavior, mule deer females may position themselves between offspring and predator before attacking the predator (Wenger 1981). In response to our own disturbance, we observed similar flight behavior of mule deer females that allowed their fawns (presumably >1.5 weeks-old) to flee in front of them before stopping to assess the threat. In other cases when we captured bedded neonates that vocalized (Atkeson et al. 1988), mule deer females often would remain nearby stomping, snorting, and even charging. Aside from fleeting curiosity, white-tailed females exhibited no such behavior. Female moose (*Alces alces*) may respond similarly and more aggressively to neonate capture than did mule deer (W. Ballard, personal observation).

Aggressive antipredator behavior of mule deer females can be cooperative (Cahalane 1947, MacConnell-Yount and Smith 1978, Lingle et al. 2005), and greater defense against coyote predation can result in significantly fewer fawn losses and possibly greater population growth rates compared to sympatric white-tailed deer (Whittaker and Lindzey 1999, 2001; Lingle et al. 2005). Our results from 2004 and 2005 supported the hypothesis that mule deer females kept fawns nearby to defend them from small predators, which resulted in lower predation rates than experienced by white-tailed deer exhibiting the loose cohesion strategy during the hider phase (Figs. 17, 19). Mule deer fawn depredation was greater in 2006 (Fig. 17), and bobcats were able to consume more of their kills that year (see Results); this may have been predictable because adult females were in poorest condition among years (Figs. 7, 12; Smith 1987).

Deer evolved reproductive biology and rearing strategies in response to environmental and predatorial influences (Bergerud 1974, Lent 1974, Rutberg 1987, Ims 1990, Geist 1998), but it is not clear how past selection for predator avoidance affects behavior in the absence of prehistoric predators (Linnell et al. 1995, Dingemanse and Réale 2005, Blumstein et al. 2006, Nussey et al. 2007). To our knowledge, we were the first to describe maternal antipredator strategy and fawn mortality of white-tailed deer in the absence of large predators such as coyotes, black bears (*Ursus americanus*), and wolves (*Canis lupus*). White-tailed deer may be the oldest extant deer species, being >3 million years-old, and prior to the late-Pleistocene extinctions, they shared North America with 15 predators larger than coyotes (Geist 1998). With such long and strong predator selection, it is understandable that much of their antipredator behavior may be innately fixed (Flecker 1992, Clark and Yoshimura 1993, Sih et al. 2004, Turner et al. 2006). However, while the loose cohesion antipredator strategy may be adaptive in the presence of large predators, it seems to be maladaptive where they are absent because extirpation of large predators may release populations of smaller predators (e.g., bobcats and foxes) that could be defended against (Henke and Bryant 1999, Jarnemo 2004).

A long-term study in Sweden demonstrated that red foxes were the primary cause of roe deer fawn mortality (Jarnemo and Liberg 2005). Roe deer are smaller than North American *Odocoileus* but evolved with wolves and lynx (*Lynx pardinus*) as primary predators that have since been extirpated (Jarnemo and Liberg 2005). Red foxes ate primarily rodents and lagomorphs and killed roe deer fawns when available but were not a threat to adults (Jarnemo 2004). Even though roe deer adults were physically capable of defending their fawns from red foxes with high rates of success, annual predation rates were as high as 90% during years with high fox abundance (Jarnemo 2004, Jarnemo and Liberg 2005). Although no actual group cohesion data were presented, descriptions of behavior suggested that roe deer females mostly chose to separate and leave their fawns (Jarnemo 2004). In contrast, in South America where large canids were prehistorically absent, the small pampas deer (*Ozotoceros bezoarticus*; about 35 kg) seemed to exhibit innate aggressive behavior towards Paraguayan fox (*Dussicyon gimmocerus*) and would even attack humans to protect fawns (Jackson 1985 cited in Geist 1998).

It is possible that mule deer employed a similar and effective maternal antipredator strategy for coyotes as they did at our site against bobcats. In Washington where coyotes were predators of fawns, 26 of 39 mule deer fawns (67%) captured were twins (Steigers and Flinders 1980), suggesting to us that postpartum grouping patterns were somewhat similar to those we reported for mule deer (Fig. 19; Haskell et al. 2007). Of 8 sets of twins with known fates, only 1 pair was killed simultaneously during a coyote attack although coyotes killed 10 fawns (Steigers and Flinders 1980). Interestingly, most coyote kills occurred after fawns were >40 days-old, apparently as coyote pups matured and formed hunting packs with adults (Steigers and Flinders 1980). Thus, active defense of fawns by mule deer females may be an effective strategy against solitary or paired coyotes but less so for packs.

It is unknown how plastic the antipredator behavioral phenotype of mule deer may be, or what predator aggregates over what period of time might elicit what type of behavior. Glacier National Park also has a sympatric population of deer with many large predator species. Such a site seems suitable for a natural experiment. Mule deer may only be several thousand years-old and the youngest extant deer species (Geist 1998). Also, because they coexisted with large predators during their relatively brief evolutionary prehistory, we predict that their maternal antipredator behavior will prove to be more flexible than that of white-tailed deer. The predator-prey behavioral interaction may not be simple. Generalist canids and ursids are the most efficient fawn predators (Linnell et al. 1995, Ballard et al. 2001). Therefore, if large felids suppress large canid or ursid populations, it may be a suitable strategy to keep fawns close to protect against smaller predators.

West Texas Deer History

Biologists have been confounded by the fall and rise of mule deer in the western U.S. It has been suggested that effects of overgrazing by livestock resulted in mule deer declines in early–mid 1900s, but the same authors noted that mule deer have rebounded in some areas despite continued overgrazing practices (Mackie 1981, Severson 1981). Curtailment of hunting overexploitation is one explanation, but probably does not fit the case in west Texas without historic demand for market hunting (Schmidly 2002). There is a similar history of Great Plains mule deer range withdrawal and recovery in the early–mid 1900s; market hunting for railroads may have had greater impact on deer of the northern Plains relative to those in west-central Texas (Severson 1981). While some biologist have noted that increased brush cover resulting from grazing practices may have improved habitats for mule deer in some areas (Short 1977), the opposite effect from brush encroachment has been suggested for west Texas (Wiggers and Beasom 1986). However, where mule deer receded from west-Texas rangelands in the late-1800s–mid-

1900s, they are now recolonizing the same areas that are still brush-dominated and occupied by white-tailed deer. It has also been hypothesized that habitat fragmentation and hybridization caused mule deer decline in west Texas (Schmidly 2004). The fragmentation hypothesis is similarly moot as that for brush encroachment. While hybridization does occur between white-tailed and mule deer in contact zones, it is at low levels, and introgression is not significant (Cronin 2003, Baker and Bradley 2006). Furthermore, breeding periods for these sympatric species were 1 month apart at our site (Haskell et al. 2008*a*).

Our data from adult female and fawn mule deer mortalities suggest that disease may be important to consider. Mule deer adults appeared to experience a lagged decline after substantial rains of 2004 and 2005 (Figs. 2, 3, 5, 12), and even when range conditions were optimal during early rearing, mule deer fawns succumbed mostly to sickness and starvation (Figs. 5, 17). Most disease reports are isolated and individualistic (review by Neiland and Dukeminier 1972). Biologists have taken note of acute localized mule deer die-offs associated with disease transmission from livestock (Leopold et al. 1951), but gradual widespread decline and chronic effects of disease may be less obvious. Bluetongue may have been partially responsible for extirpation of bighorn sheep (*Ovis canadensis*) from southwest Texas (Robinson et al. 1967), and there is anecdotal evidence that livestock diseases periodically decimated pampas deer in South America (Jackson and Langguth 1987). After the phenomenal rains of 2004, stocking rates of livestock were markedly increased on all 4 ranches (S. Haskell, personal observation).

Deer with briefer evolutionary history may be more susceptible to pathogens (Geist 1998). In a more immediate context, European settlement of North America occurred from east to west, so white-tailed deer were exposed to livestock-borne pathogens before mule deer. If our hypothesis that livestock-borne pathogens caused the historic decline of mule deer in west Texas is valid, then the fact that mule deer are rebounding is evidence that adaptation of immunocompetence may be an innate characteristic requiring exposure and not necessarily relying on natural selection (Gaydos 2005), although it is plausible that selection does still occur. For example, we captured all the fawns produced in the life of a mule deer that succumbed to sickness-starvation at 4 years-old in 2006; her twins died near birth in 2004 (Appendix A photo no. 2), her singleton died from a head infection in 2005 (Appendix A photo no. 9), and her twins were killed by bobcats in 2006. Nearly all of our adult deer tested positive hemorrhagic disease titers, but mule deer fawns were still the group most afflicted by disease. Because deer population trajectory is most sensitive to adult female mortality (Gaillard et al. 2000, Haskell and Ballard 2007*a*), high survival of mule deer adults during extended drought periods when vectors such as *Culicoides* are reduced may have facilitated their recovery (Figs. 3, 12). Mule deer may eventually achieve the enzootic stability (i.e., rarely showing clinical signs despite antibody sero-prevalence) seemingly exhibited by white-tailed deer in this region (2004 and 2005 in Fig. 17; Stallknecht et al. 1996, Gaydos 2005).

Hemorrhagic disease can be peracute, acute, or chronic, and clinical signs have been recognized in *Odocoileus* since the late 1800s (Nettles and Stallknecht 1992, Davidson and Nettles 1997). Acute and fatal population-level outbreaks in mule deer, and particularly white-tailed deer, have made BT and EHD 2 of the most studied diseases of deer (Nettles and Stallknecht 1992, Howerth et al. 2001), yet new and related viruses are still being discovered (Woods 2001, Gaydos 2005).

Regarding comparative susceptibility of these species to hemorrhagic diseases, our results seem discordant with some literature. On the northern Great Plains in areas of North Dakota and Canada, periodic epizootics of hemorrhagic disease have killed more white-tailed deer than mule deer where they are sympatric (Ditchfield et al. 1964, Hoff et al. 1973). However, habitat relationships should be considered. In the more studied white-tailed deer, epizootic frequency declines but severity increases with latitude as the climate becomes less favorable for the *Culicoides* vectors that thrive with warmer climate (Nettles and Stallknecht 1992, Davidson and Doster 1997, Smith and Mullens 2003, Gaydos 2005). Repeated exposure to the virus is thought to produce high prevalence of neutralizing antibodies and possibly enzootic stability in extreme cases such as Texas (Nettles and Stallknecht 1992, Stallknecht et al. 1996, Davidson and Doster 1997, Gaydos 2005). Also, *Culicoides* thrive in wet environments with leaf litter (Schmidtmann et al. 1998, Paradise 2004). Where sympatric on the Great Plains and nearby mountainous regions, white-tailed deer tend to inhabit the riparian areas with greater vegetative cover, and mule deer tend to be in the more open and drier areas (Martinka 1968, Krämer 1973, Dusek et al. 1989, Mackie et al. 1998, Lingle 2002). Thus, white-tailed deer likely cohabitate with *Culicoides* more than mule deer, so when occasional but severe epizootics occur, it may be white-tailed deer that are more exposed.

Hemorrhagic diseases may not even have been responsible for most disease related deaths (Appendix A, Fig. 9). Viral and bacterial diseases can be interactive along with starvation and predation (Davidson and Doster 1997, Williams and Barker 2001, Wobeser 2006). Blood results were negative for IBR in 2004, but in April 2006, we noted vaginitis that is characteristic of IBR in a barren mule deer. Sera were also negative for BVD antibodies in 2004, but serum testing for the BVD *Pestivirus* may not detect antibody titers for similar pathogenic pestiviruses (Van Campen et al. 2001). We observed several incidences of mummified fetuses and stillbirths that are characteristic of the pestiviruses (Van Campen et al. 2001). There were many potential pathogens for which we did not test, including *Herpesvirus* that is responsible for malignant catarrhal fever and hosted by domestic sheep which were implicated post hoc by our weaning data as a particularly problematic pathogenic agent (Appendices A, B). In this semiarid environment, animals from numerous taxa (e.g., javelinas, opossums, skunks, raccoons, foxes, bobcats, livestock, deer, vultures, etc.) use water troughs characterized by some overflow and mud (O'Brien et al. 2006; S. Haskell, personal observation). With the advent of barbed wire and windmill water-tanks around 1900 (Schmidly 2002), we suspect that these fixed locations became important for disease transfer (Fig. 1), and the disappearance of mule deer ensued.

MANAGEMENT IMPLICATIONS

The sympatric populations of white-tailed and desert mule deer in northwest Crockett County, Texas appear to respond to a carrying capacity that fluctuates seasonally and annually with precipitation. We recommend a reduction in the herd to about one-half its current density of about 30 deer/km^2. However, reduction in deer density alone would likely be insufficient to allow long-term improvement in habitat conditions unless other herbivores are reduced as well. Ranching domestic sheep has necessitated extensive predator control on these private lands because predators such as coyotes can kill lambs and adults (Knowlton et al. 1999, Sacks et al. 1999, Blejwas et al. 2002, Sacks and Neal 2002). Switching to cattle-only operations would not only reduce direct forage competition between livestock and deer (Julander 1955, McMahan 1964, Teer 1984), but would also permit coexistence of coyotes and cow-calf operations because many cattle breeds are effective at defending their young from such predators (L.D. Clark, former ATA ranch manager, personal communication). Coyotes may in turn directly or indirectly reduce overabundant rodents and lagomorphs that likely compete with deer and livestock for spring and summer forbs during critical late gestation and lactation periods (Taylor 1930, Taylor et al. 1935, Mackie 1970, Henke and Bryant 1999, Schmidly 2002). Coyotes could also be expected to kill fawn and adult deer (Linnell et al. 1995, Ballard et al. 2001), thus benefiting livestock directly and deer indirectly.

Poor grazing management practices exacerbated by drought can have significant impact on wild ungulate ecology and population vital rates (Taylor and Hahn 1947, McMahan and Ramsey 1965, Hailey et al. 1966, Jenks and Leslie 2003, Haskell et al. 2008*a*). Rotational and moderate grazing during drought and wet periods may help improve range for livestock and deer (Young 1956, Reardon and Merrill 1976, Thurow et al. 1988, Ragotzkie and Bailey 1991, Thurow and Taylor 1999), potentially increasing the economic value of deer to private landholders (Sanders 1941, French et al. 1965, Ramsey 1965, Butler and Workman 1993, Schultz and Johnson 19995, Schmidt et al. 2007). However, given the consistency of historic human land-use practices in this region of central Texas, human social constraints will likely continue to prevent effective deer management (Sanders 1941, Taylor and Hahn 1947, Teer et al. 1965, Cook 1984, Teer 1984).

Given that deer management on private rangelands is beyond the capability of TPWD, we recommend that less effort be expended on deer surveys and more effort be expended elsewhere. In particular, the rangeland, wildlife, and landholders may benefit from research into alternative economic means provided from the land and public outreach and ecological education (Cassidy and Grue 2000, Loomis 2000, Benson 2001, Brown 2001, Morrisette 2001). There are now relatively few cowboys that grow up on horseback and learn to understand and respect the land, and even these individuals are rarely responsible for land management decisions (L.D. Clark, former ATA ranch manager, personal communication). Also, with an overabundance of small mammal prey, high reproductive rates, and rapid home-range settling by transient bobcats (Fritts and Sealander 1978, Winegarner and Winegarner 1982, Litvaitis et al. 1987), federal monies seem ill spent shooting bobcats from helicopters on these private lands. The result of such predator-culling operations is counterproductive, at least temporarily, with more deer and lagomorphs to compete with livestock.

It may be of management importance to understand ramifications of maternal antipredator behavior if reduction of larger predators releases populations of smaller predators (Henke and Bryant 1999). If management objectives are to increase fawn survival then drastic reduction of large predators may have undesirable results if the deer species exhibits innately-fixed loose cohesion maternal antipredator behavior, such as white-tailed and roe deer.

SUMMARY

1. Data from adult female survival and weights and fawn survival, thymus glands, weight gain, hoof growth (Haskell et al. 2007), birth dates (Haskell et al. 2008*a*),

and weaning dates indicated that this deer population was chronically stressed near a carrying capacity that responded to rain and that females invested relatively little energy rearing fawns. We implicate overgrazing and predator extirpations and removal, which is concordant with findings >50 years ago (Taylor and Hahn 1947, Teer et al. 1965). If allowed, coyotes may be expected to directly or indirectly reduce overabundant deer, lagomorph, and rodent populations (Henke and Bryant 1999, Ballard et al. 2001), thus reducing forage competition for both deer and livestock and increasing profits for landholders.

2. White-tailed deer appeared more stressed by drought, and mule deer more susceptible to disease. While cattle are known carriers of some pathogens present at our site, domestic sheep appeared to be a particular problem. We hypothesize that mule deer disappeared from most of west Texas between the mid-1800s and -1900s because they were naïve to livestock-borne pathogens. Common use of water tanks by many taxa likely promotes disease transfer.
3. In general, bobcats as the primary predator killed healthy fawns, making this mortality source directly additive. However, there was evidence of some direct compensatory mortality with bobcats taking unhealthy fawns. Furthermore, top-down limitation was negligible in the adult portion of the population, so by taking fawns, bobcats provided the only important top-down influence. Thus, in a long-term context, fawn depredation by bobcats may be to some degree compensatory by mitigating negative consequences of density-dependent population vital rates that respond to a rapidly changing carrying capacity via rain.

4. Some salient results from the fawn mortality study included: 1) reduced rain during late gestation and lactation increased rates of sickness-starvation and predation, though increased predation may have been somewhat compensatory, 2) relatively heavy fawns survived better soon after birth, 3) mule deer fawns succumbed to sickness-starvation more than did white-tailed fawns, 4) male fawns >30 days-old succumbed to sickness-starvation more than did females which accounted for skewed sex ratios in the adult population, 5) increased deviation from mean birth date increased risk of predation and sickness-starvation, and 6) we found no evidence an adult female social dominance effect (i.e., age) on fawn survival.
5. In 2004 and 2005 when adult females were in best condition, postpartum mule deer kept fawns nearby and close together to protect them from small predators. In contrast, postpartum white-tailed females separated their fawns and remained distant from them. The loose cohesion strategy of white-tailed deer was maladaptive in the absence of large predators, as they experienced greater fawn depredation by bobcats; this behavior may be the result of a relatively long evolutionary history with many large predators. It is unknown how flexible postpartum antipredator strategies may be for mule deer in the presence of large predator aggregates.
6. We found that on more overgrazed ranches, female deer birthed later (Haskell et al. 2008*a*) and produced more males that were prematurely weaned more than females, thus making males more susceptible to sickness-starvation when >30 days-old.

7. Effective deer management is impossible on these private lands when predators of adult deer are eliminated, hunters do not provide a top-down influence, and human land-use practices affect deer ecology and population vital rates across fence-lines.
8. It has been almost a century since wildlife management was formalized (Leopold 1933). The deer herds of west-central Texas were unhealthy then and are likely to remain so until we popularize the land ethic and teach our stakeholders and beneficiaries how to think like a mountain (Sanders 1941, Leopold 1966, Teer 1984, Schmidly 2002). Ecological education needs to be from grades K–12 (Dingell and Potter 1978, American Association for the Advancement of Science 1993, Vitousek 1994, Blank et al. 2003), and we need to reach all segments of society (Schmidly 2002). While incentive programs for private land-holders are various and have potential for success (Schmidly 2002), they are abused (S. Haskell, personal observation), so more focus should be given to developing alternative economic resources on private lands to promote sustainability and positive ecosystem feedbacks (e.g., water-soil-plant cycles) that are beneficial not detrimental.

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Table 6.1. Research hypotheses and predictions for a study of sympatric white-tailed and desert mule deer in west-central Texas, 2001–2007.

Hypothesis	Prediction
The deer population exists near a carrying capacity that responds to precipitation.	Annual adult female survival (along with fawn survival) will fluctuate with precipitation.
White-tailed deer are more susceptible to drought than are desert mule deer.	There will be > interannual variation in survival rates of white-tailed deer than for mule deer.
Autumn fawn:female ratios were positively correlated with spring rain because vegetation is needed for nutrition and not hiding cover for fawns.	Adult fecundity will be high regardless of rain. Variable fawn survival rates in response to precipitation will be due more to changes in sickness-starvation than predation.
Adult female social rank will affect fawn survival, thus creating potential for a behavioral carrying capacity.	After accounting for adult female condition in fawn survival models, female age (possibly quadratic) will still be a useful predictor.
Fawn predation is additive mortality in a short-term context.	After accounting for fawn age, thymus glands from predator-killed fawns will weigh more than those from fawn succumbing to sickness-starvation.
At our site, adult females invest relatively little energy in rearing their fawns.	Fawns will have relatively low weight gain and will be weaned early.
Postpartum mule deer females are more aggressive towards predators than are white-tailed females.	Mule deer will keep fawns closer to themselves and each other. Kill-sites will show evidence of maternal defense by mule deer.
The separate-and-hide strategy by white-tailed females is maladaptive in the absence of large predators.	White-tailed fawn mortality due to predation during the hider phase will be > than that for mule deer fawns.

Table 6.2. Models explaining weights of adult female white-tailed and mule deer captured in Crockett County, Texas, April 2004–2006. Parameters include species (1), year (2), location (3), age (4), age^2 (5), and species×year (6).

Parameters	R^2_{LR}	-2LogL	AIC	AICc	ΔAICc	w_i
1,2,4,5	0.791	797.8	813.8	814.8	0.0	0.556
1,2,3,4,5	0.796	796.2	814.2	815.5	0.7	0.391
1,2,3,4,5,6	0.798	795.7	817.7	819.5	4.7	0.053
2,4,5	0.677	826.6	840.6	841.4	26.6	0.000
1,2,4	0.532	851.1	865.1	865.8	51.0	0.000
4,5	0.238	883.3	893.3	893.7	78.9	0.000
4	0.053	897.6	905.6	905.8	91.0	0.000
intercept-only	0.000	901.2	907.2	907.3	92.5	0.000

Table 6.3. Preferred model explaining weights (kg) of adult female white-tailed and mule deer captured in northwest Crockett County, Texas, April 2004–2006. Reference levels for categorical variables are white-tailed deer for species and 2006 for year. Effects after intercept in order of decreasing partial significance.

Parameter	Estimate	SE	df	t	Pr > |t|
Intercept	38.009	1.580	89	24.06	<0.001
Age^2	-0.300	0.037	130	-8.04	<0.001
Age	3.830	0.483	118	7.93	<0.001
Year '04	5.426	0.682	142	7.95	<0.001
Year '05	4.568	0.503	140	9.09	<0.001
Species	6.232	1.033	64.3	6.03	<0.001

Table 6.4. Models explaining survival rates of adult female white-tailed and mule deer captured in Crockett County, Texas, May 2000–April 2002 (dry period) and May 2004–April 2007 (wet period). Parameters include species (1), period (2), and species×period (3).

Parameters	R^2_{LR}	-2LogL	AIC	AICc	ΔAICc	w_i
1,2,3	0.355	333.1	339.1	340.0	0.0	0.931
none	0.000	346.7	346.7	346.7	6.7	0.033
1	0.050	345.1	347.1	347.2	7.2	0.025
2	0.001	346.6	348.6	348.8	8.8	0.011
1,2	0.051	345.1	349.1	349.5	9.5	0.008

Table 6.5. Models explaining gender of white-tailed (*n*=53) and mule deer (*n*=87) fawns captured in Crockett County, Texas, summers 2004–2006. Parameters include no. offspring (1), ranch location (2), relative adult female weight (3), species (4), year (5), adult female age (6), age^2 (7), and species×year (8).

Parameters	R^2_{LR}	-2LogL	AIC	AICc	ΔAICc	w_i
1,2	0.063	183.1	189.1	189.3	0.0	0.414
1,2,3	0.071	182.0	190.0	190.3	1.0	0.250
1	0.036	187.1	191.1	191.2	1.9	0.158
intercept-only	0.000	192.2	194.2	194.3	5.0	0.034
1,2,3,4	0.073	181.7	191.7	192.1	2.9	0.099
1,2,3,4,6	0.074	181.5	193.5	194.1	4.8	0.037
1,2,3,4,5,6	0.076	181.1	197.1	198.2	8.9	0.005
1,2,3,4,5,6,7	0.076	181.1	199.1	200.5	11.2	0.002
global	0.080	180.5	202.5	204.6	15.3	0.000

Table 6.6. Models explaining weights of white-tailed (*n*=53) and mule deer (*n*=86) fawns captured in Crockett County, Texas, summers 2004–2006. Parameters include no. offspring (1), ranch location (2), relative adult female weight (3), species (4), year (5), natural logarithm of fawn age at capture(6), adult female age (7), age^2 (8), and species×year (9).

Parameters	R^2_{LR}	-2LogL	AIC	AICc	ΔAICc	w_i
1,3,4,5,6,7	0.291	209.8	227.8	229.2	0.0	0.530
1,3,4,6	0.252	217.3	229.3	229.9	0.7	0.378
1,3,4,5,6,7,8	0.298	208.4	228.4	230.1	0.9	0.346
1,3,4,5,6	0.273	213.2	229.2	230.3	1.1	0.308
1,2,3,4,5,6,7,8	0.305	207.0	229.0	231.0	1.8	0.215
1,4,6	0.224	222.4	232.4	232.9	3.7	0.085
global	0.314	205.2	231.2	234.1	4.9	0.046
1,6	0.156	234.0	242.0	242.3	13.1	0.001
6	0.107	241.9	247.9	248.1	18.9	0.000
intercept-only	0.000	257.6	261.6	261.7	32.5	0.000

Table 6.7. Preferred model explaining weights (kg) of white-tailed (*n*=53) and mule deer (*n*=86) fawns captured in northwest Crockett County, Texas, summers 2004–2006. Explanatory variables include the natural logarithm of fawn age at capture (days), no. of offspring, species, year, individual residual from the preferred adult female weight model (kg), and adult female age. Reference levels for categorical variables are white-tailed deer for species and 2006 for year. Effects after intercept in order of decreasing partial significance.

Parameter	Estimate	SE	χ^2_1	Pr > χ^2
Intercept	3.727	0.256	211.54	<0.001
Fawn age	0.207	0.049	17.89	<0.001
No. offspring	-0.498	0.129	14.89	<0.001
Species	0.325	0.095	11.72	0.001
Year '04	-0.200	0.125	2.57	0.109
Year '05	0.098	0.106	0.85	0.356
Adult weight	0.020	0.010	3.65	0.056
Adult age	-0.042	0.023	3.42	0.065

Table 6.8. Potential factors (with references) affecting survival of white-tailed and mule deer fawns captured in northwest Crockett County, Texas, 2004–2006. All factors combined additively represent the global model for time-independent Cox proportional hazards regression.

Covariate	References
Species	Whittaker and Lindzey 1999
Total rain May–Aug	Teer et al. 1965, Ginnett and Young 2000
Species×rain interaction	Anthony and Smith 1977, Brown and Henry 1981
Absolute deviation from mean birth date by species and year	Whittaker and Lindzey 1999, Jarnemo et al. 2004
Gender	Heffelfinger et al. 2003
Residual from best adult female weight model	Verme 1962, Andersen and Linnell 1998
Residual from best fawn weight model	Verme 1977, Raganelia-Pelliccioni et al. 2006
Adult female age (quadratic to start)	Ozoga et al. 1982, Ozoga and Verme 1986*b*
No. offspring	Andersen and Linnell 1998
Ranch location	Haskell et al. 2008*a*

Table 6.9. Models explaining survival of white-tailed and mule deer fawns captured in Crockett County, Texas, summers 2004–2006. Parameters include no. offspring (1), ranch location (2), relative adult female weight (3), species (4), total rain from May–Aug (5), fawn gender <30 days-old (6), fawn gender ≥30 days-old (7), deviation from mean birth date (8), relative fawn weight (9), fawn weight×natural logarithm of event time (10), adult female age (11), age^2 (12), and species×rain (13).

Parameters	R^2_{LR}	-2LogL	AIC	AICc	ΔAICc	w_i
5,7,8,9,10	0.359	767.9	777.9	778.5	0.0	0.363
2,5,7,8,9,10	0.369	766.3	778.3	779.2	0.7	0.259
2,5,7–11	0.379	764.8	778.8	780.0	1.5	0.170
1,2,5,7–11	0.389	763.1	779.1	780.8	2.2	0.118
1,2,5,7–12	0.393	762.4	780.4	782.5	4.0	0.050
1,2,4,5,7–12	0.398	761.7	781.7	784.2	5.7	0.021
1–5,7–12	0.402	761.1	783.1	786.1	7.6	0.008
7,8,9,10	0.289	778.0	786.0	786.4	7.9	0.007
1–12	0.402	761.0	785.0	788.6	10.1	0.002
global	0.409	759.8	785.8	790.2	11.6	0.001
7,8,9	0.198	789.8	795.8	796.1	17.6	0.000
7,8	0.177	792.3	796.3	796.5	17.9	0.000
8	0.066	804.8	806.8	806.8	28.3	0.000
none	0.000	811.4	811.4	811.4	32.9	0.000

Table 6.10. Preferred model explaining hazards for white-tailed and mule deer fawns captured in northwest Crockett County, Texas, summers 2004–2006. Explanatory variables include the absolute deviation from mean birth date by species and year (days), gender ≥30 days postpartum (females as reference), individual residual from best fawn weight model (kg, Table 7), fawn weight×natural logarithm of mortality event time (days), and total rain from May–Aug during the late gestation and lactation period (cm). Effects in order of decreasing partial significance and 95% CI for hazard ratios included.

Parameter	Estimate	SE	χ^2_1	Pr > χ^2	Hazard ratio	LCI	UCI
Birth date	0.048	0.012	16.74	<0.001	1.05	1.03	1.07
Gender	1.316	0.335	15.41	<0.001	3.73	1.93	7.19
Fawn weight	-1.057	0.272	15.11	<0.001	0.35	0.20	0.59
Weight×time	0.327	0.103	10.06	0.002	1.39	1.13	1.70
Rain	-0.059	0.019	9.65	0.002	0.94	0.91	0.98

Table 6.11. Models explaining cause-specific mortality of white-tailed and mule deer fawns captured in Crockett County, Texas, summers 2004–2006. Parameters include absolute deviation from mean birth date (1), fawn gender ≥30 days-old (2), relative fawn weight (3), fawn weight×natural logarithm of event time (4), total rain from May–Aug (5), species (6), and species×rain (7). Mortality type for covariate effect identified as P=predation and S=sickness-starvation.

Parameters	R^2_{LR}	-2LogL	AIC	AICc	ΔAICc	w_i
1PS,2PS,3S,4S,5PS,6S	0.459	850.3	868.3	870.4	0.0	0.415
1–3PS,4S,5PS,6S	0.469	848.5	868.5	871.1	0.7	0.286
1–3PS,4S,5PS,6S,7S	0.472	847.8	869.8	873.0	2.6	0.111
1PS,2PS,3S,4S,5P,6S	0.422	856.4	872.4	874.1	3.7	0.066
1–3PS,4S,5PS,6PS,7S	0.479	846.6	870.6	874.4	4.0	0.056
1P,2PS,3S,4S,5P,6S	0.402	859.6	873.6	874.9	4.5	0.043
1–6PS,7S	0.480	846.5	872.5	877.1	6.7	0.015
1P,2PS,3S,4S,5P	0.355	866.8	878.8	879.7	9.3	0.004
global	0.481	846.4	874.4	879.7	9.3	0.004
1P,2PS,3S,4S	0.306	873.5	883.5	884.2	13.8	0.000
2PS,3S,4S	0.277	877.4	885.4	885.9	15.5	0.000
2P,3S,4S	0.212	885.5	891.5	891.8	21.4	0.000
3S,4S	0.191	888.0	892.0	892.2	21.8	0.000
none	0.000	907.9	907.9	907.9	37.5	0.000
3S	0.001	907.9	909.9	909.9	39.5	0.000

Table 6.12. Preferred model explaining cause-specific hazards for white-tailed and mule deer fawns captured in northwest Crockett County, Texas, summers 2004–2006. Explanatory variables include the absolute deviation from mean birth date by species and year (days), gender ≥30 days postpartum (females as reference), individual residual from best fawn weight model (kg, Table 7), fawn weight×natural logarithm of mortality event time (days), total rain from May–Aug during the late gestation and lactation period (cm), and species (mule deer as reference). Effects in order of decreasing partial significance within each mortality type (P=predation, S=sickness-starvation), and 95% CI for hazard ratios included.

Parameter	Estimate	SE	χ^2_1	Pr > χ^2	Hazard ratio	LCI	UCI
Rain P	-0.094	0.022	17.69	<0.001	0.91	0.87	0.95
Gender P	1.424	0.357	15.88	<0.001	4.15	2.06	8.37
Birth date P	0.046	0.014	10.52	0.001	1.05	1.02	1.08
Fawn weight S	-1.229	0.449	7.49	0.006	0.29	0.12	0.71
Weight×time S	0.499	0.128	15.13	<0.001	1.65	1.28	2.12
Gender S	1.309	0.393	11.08	0.001	3.70	1.71	8.00
Birth date S	0.044	0.018	6.28	0.012	1.05	1.01	1.08
Species S	-0.623	0.291	4.58	0.032	0.54	0.30	0.95
Rain S	-0.052	0.026	3.90	0.048	0.95	0.90	1.00

Table 6.13. Preferred model explaining thymus gland weights (g) of dead white-tailed and mule deer fawns captured in northwest Crockett County, Texas, summers 2004–2006. Explanatory variables include the natural logarithm of fawn age at death (days) and cause of mortality (sickness-starvation as reference vs predation and other). The modeled response was log-transformed.

Parameter	Estimate	SE	χ^2_1	Pr > χ^2
Intercept	-1.842	0.373	24.35	<0.001
Fawn age	0.469	0.145	10.48	0.001
Cause of death	0.817	0.397	4.23	0.040

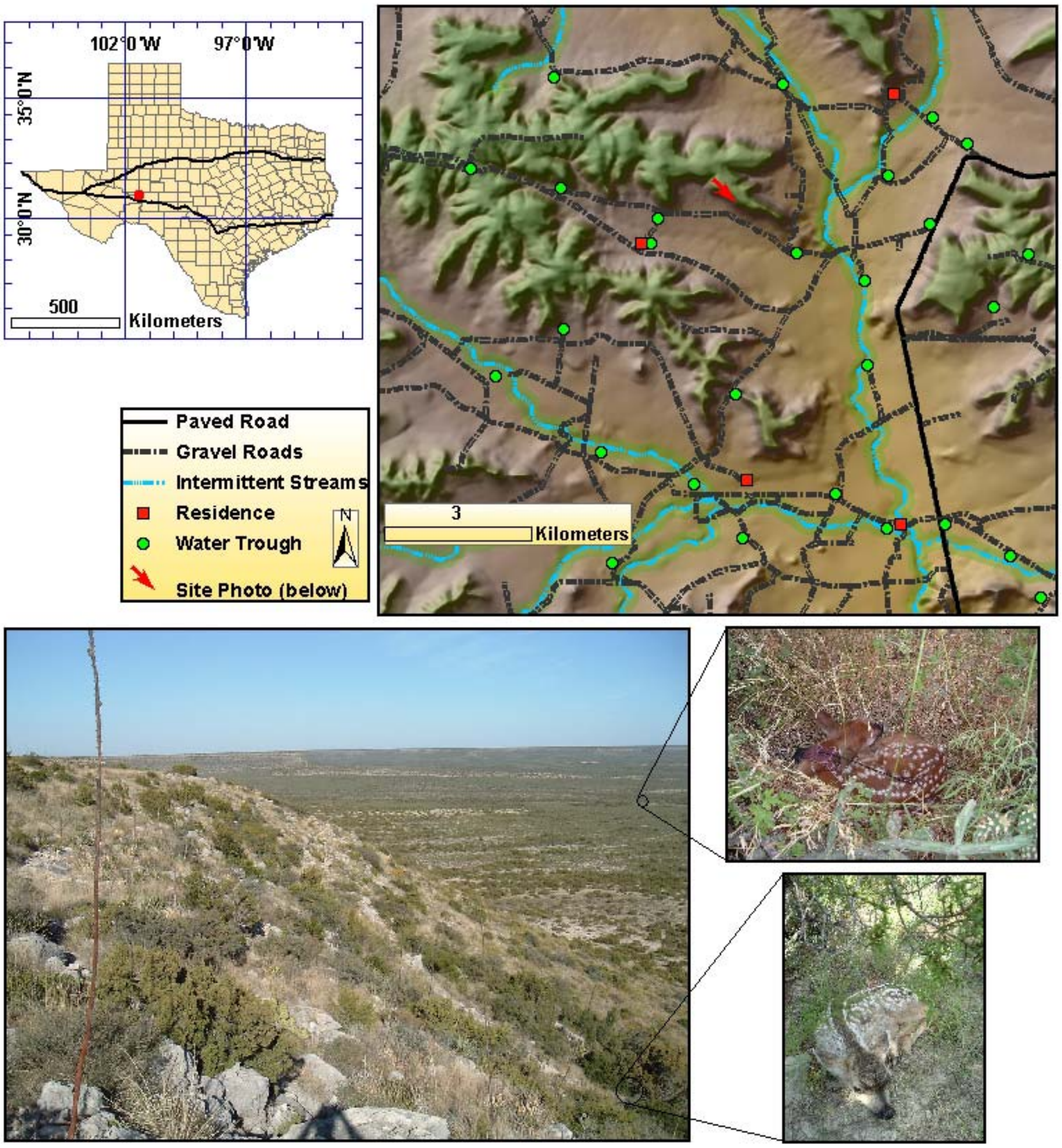

Figure 6.1. Location and features of the study site used to examine cause-specific fawn mortality of sympatric white-tailed and desert mule deer from 2004–2007 in northwest Crockett County, Texas. Adjacent lands to the north, south, and west were also used during the study of adult female survival from 2000–2003. Lines shown across Texas are highways I-20 (top) and I-10 (bottom); dot is study site. White-tailed (top) and mule deer (bottom) fawns shown in typical habitats in 2004.

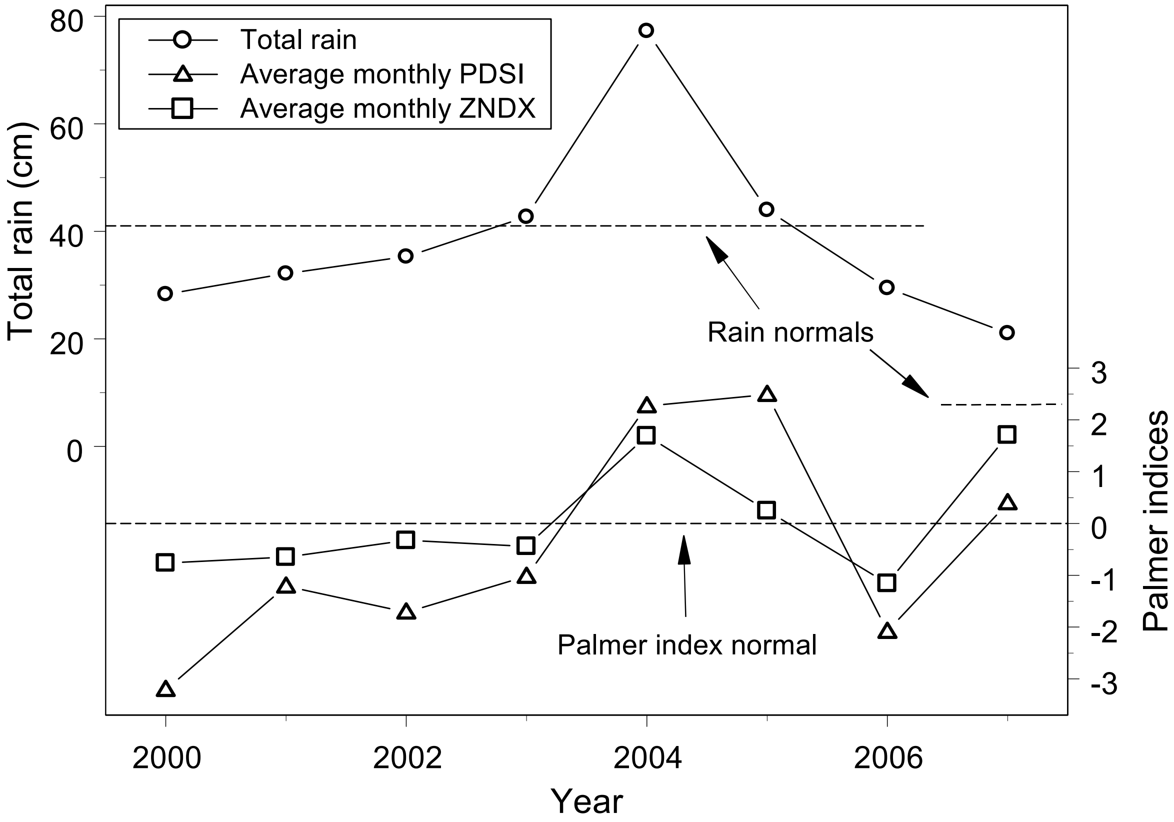

Figure 6.2. Total annual rain from 2000–2007 in northwest Crockett County, Texas, determined by summing monthly averages from 5 NOAA weather stations <60 km from the study site. Annual monthly means of the Palmer Drought Severity Index (PDSI) and Palmer Moisture Anomaly Index (ZNDX) averaged from Edwards Plateau and Trans Pecos regions. Data for 2007 from Jan–April only as reflected by rain departure from normal and Palmer indices.

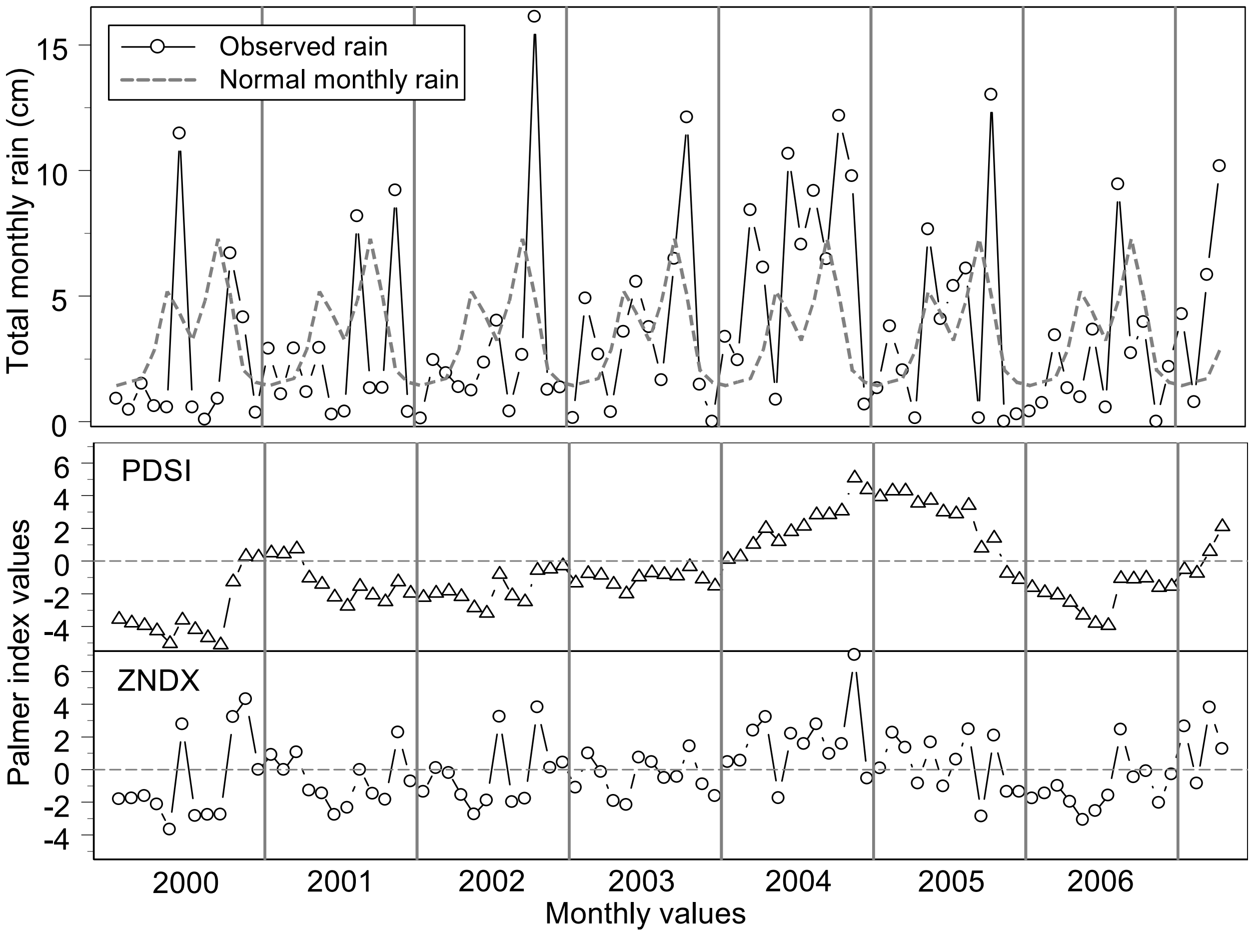

Figure 6.3. Total monthly rain from January 2000–April 2007 in northwest Crockett County, Texas, as the mean from 5 NOAA weather stations <60 km from the study site. Monthly means of the Palmer Drought Severity Index (PDSI) and Palmer Moisture Anomaly Index (ZNDX) from the Edwards Plateau and Trans Pecos regions.

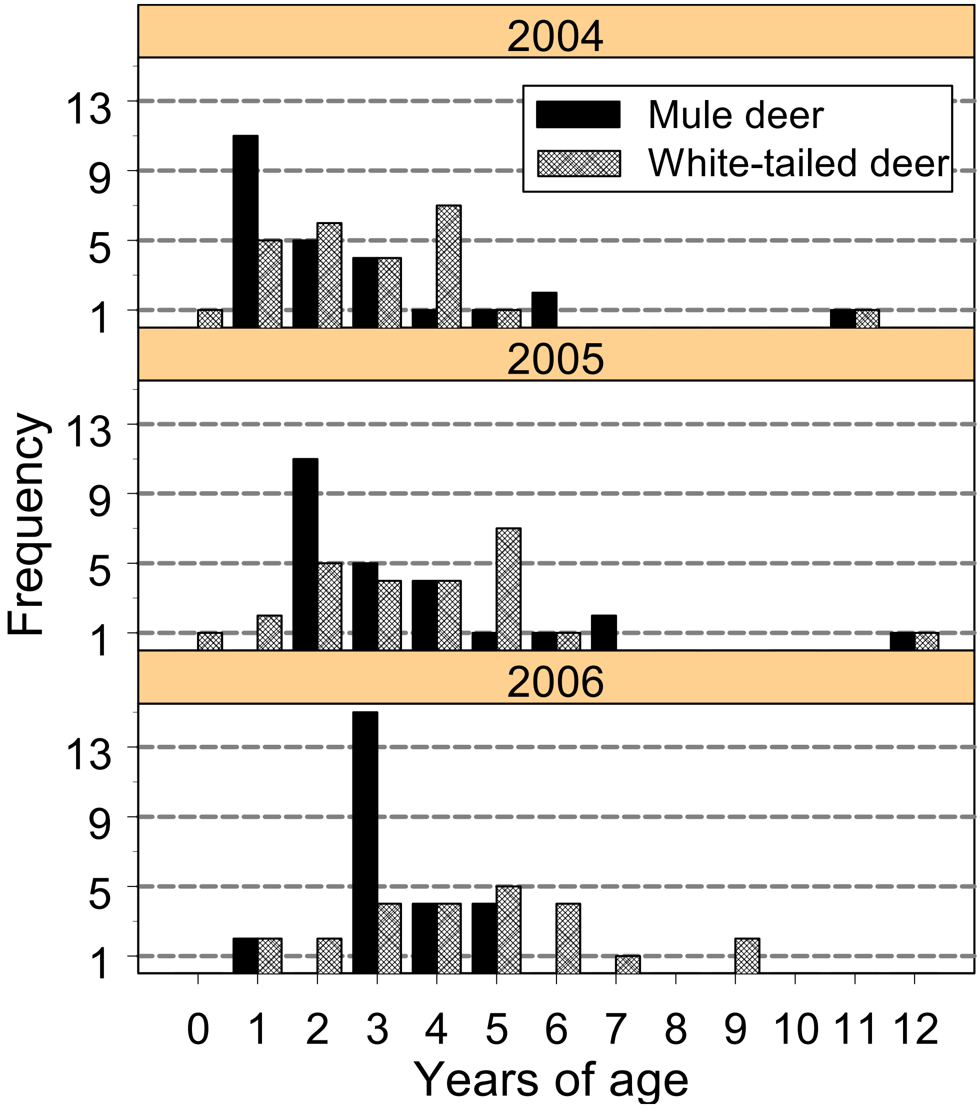

Figure 6.4. Age of female deer captured in April 2004–2006 and participating in the fawn mortality study. "Years of age" represents breeding age or the number of birthdays passed at capture with births occurring from May–August. Not included is 1 old white-tailed deer from which we did not pull a tooth and estimated her age to be 14 years-old in 2006.

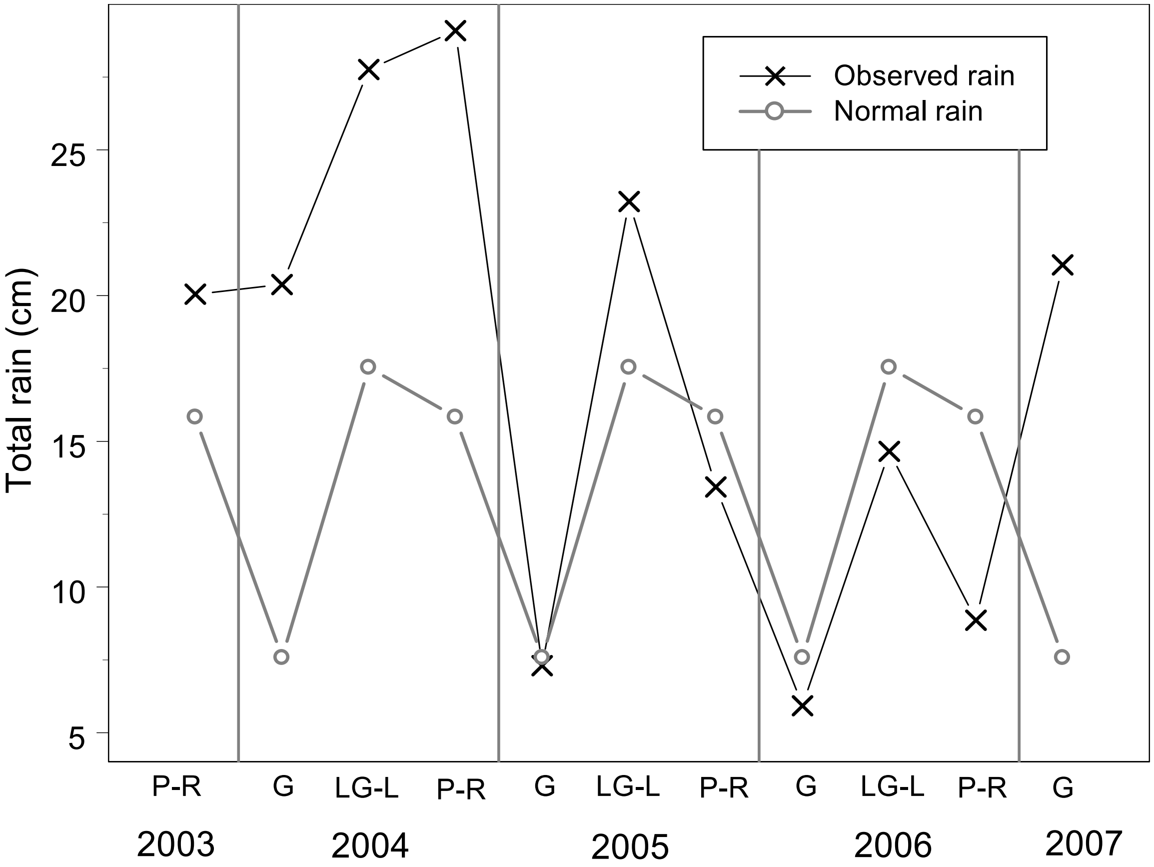

Figure 6.5. Observed versus normal total rains during the pre-rut and rut (P-R; September–December), gestation (G; January–April), and late gestation and lactation (LG-L; May–August) periods from 2003–2007 that will be useful to assess factors affecting annual recruitment and adult female weights in April.

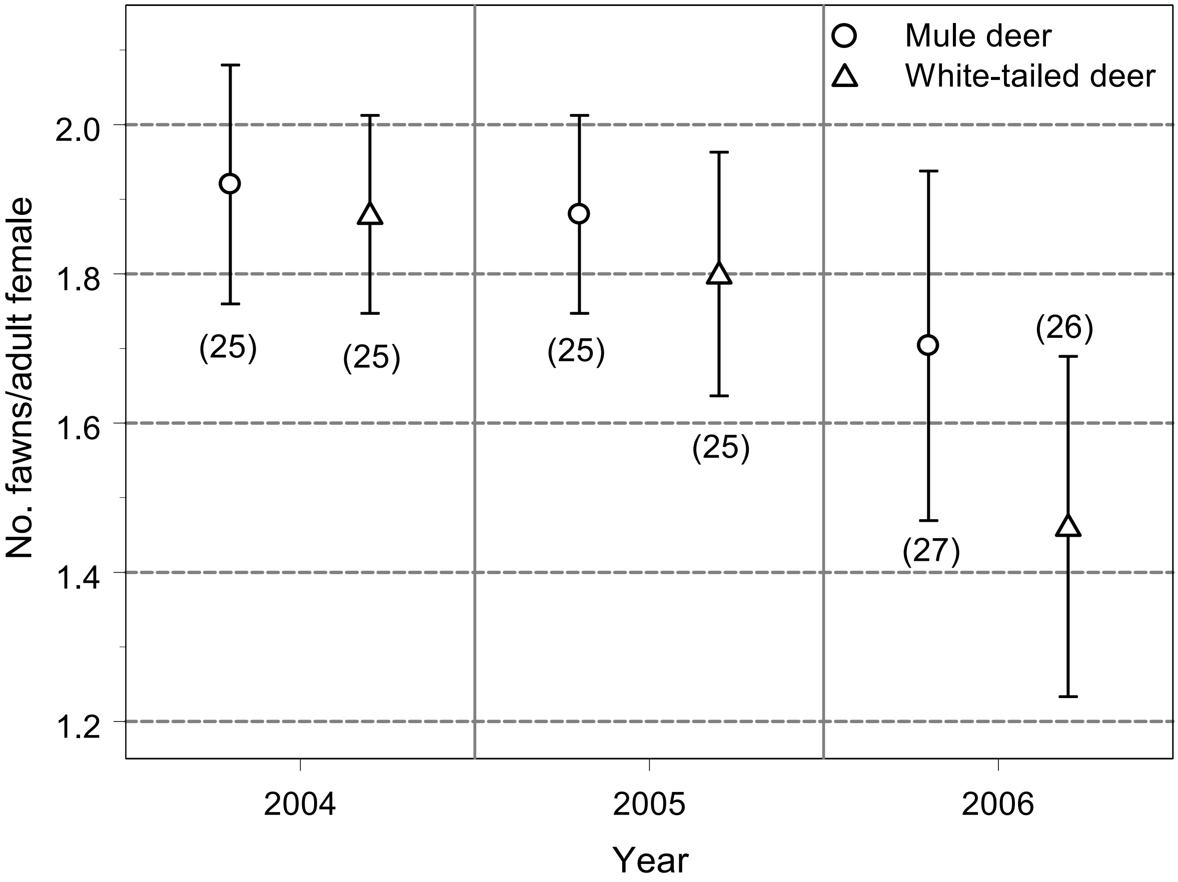

Figure 6.6. Mean reproductive rates (± 2 SE) of adult female mule deer and white-tailed deer from 2004–2006 in northwest Crockett County, Texas. Fetus counts made by ultrasonography in April and verified or corrected opportunistically during subsequent fawn capture operations in May–August.

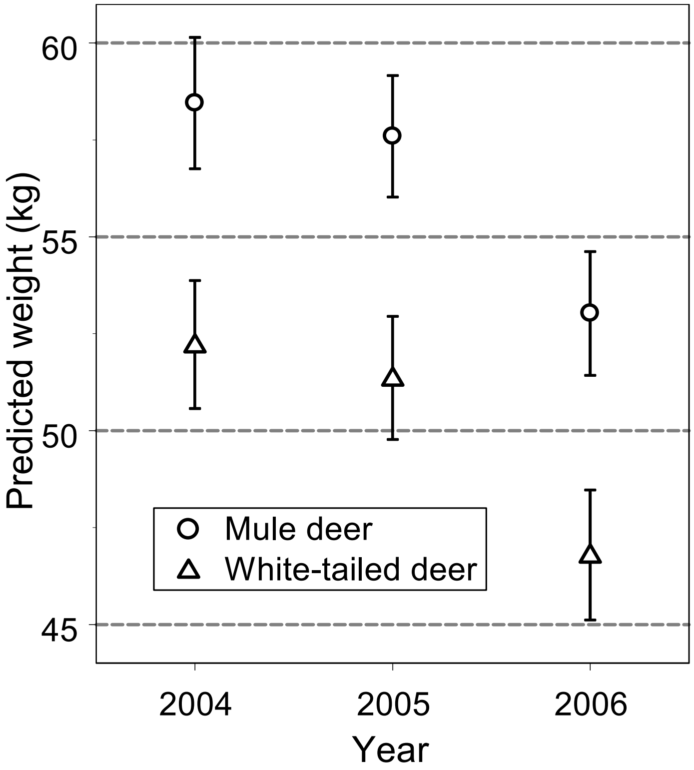

Figure 6.7. Model-predicted weights (95% CI) of 3-yr-old female mule deer and white-tailed deer captured in April 2004–2006 in northwest Crockett County, Texas.

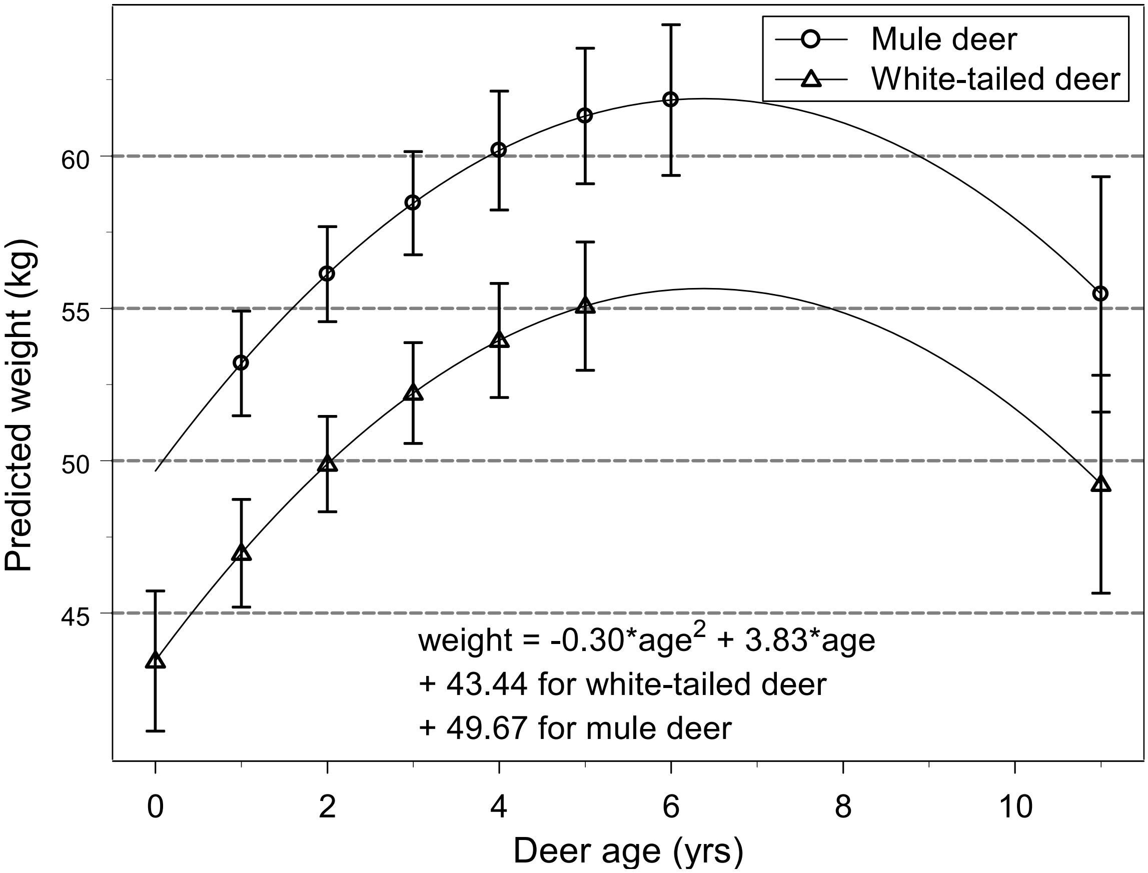

Figure 6.8. Model-predicted weights (95% CIs for ages represented in sample) by age of female mule deer and white-tailed deer captured in April 2004–2006 in northwest Crockett County, Texas. Predictions are specific to 2004; quadratic equation remains same among years except that intercepts change (Table 3).

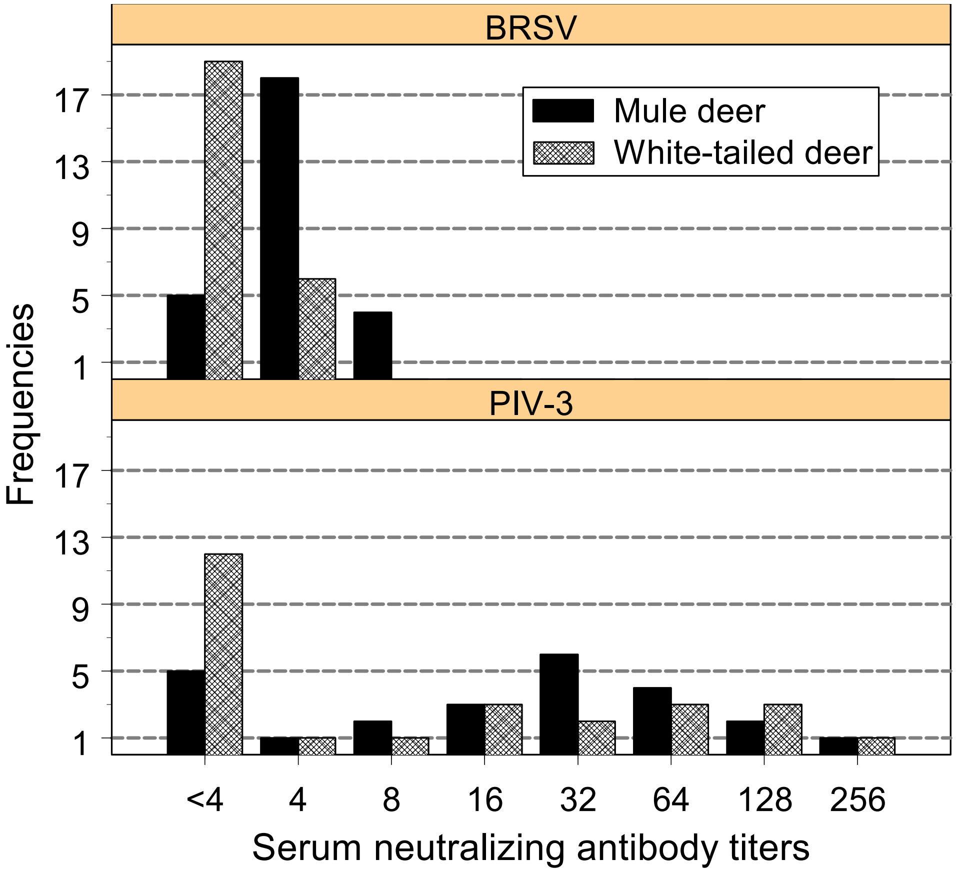

Figure 6.9. Frequency and level of serum neutralizing antibody titers for parainfluenza (PIV-3) and bovine respiratory syncytial virus (BRSV) in 25 mule deer and 25 white-tailed deer females captured in northwest Crockett County, Texas, April 2004. Titer levels <4 indicated no recent infections (Van Campen and Early 2001).

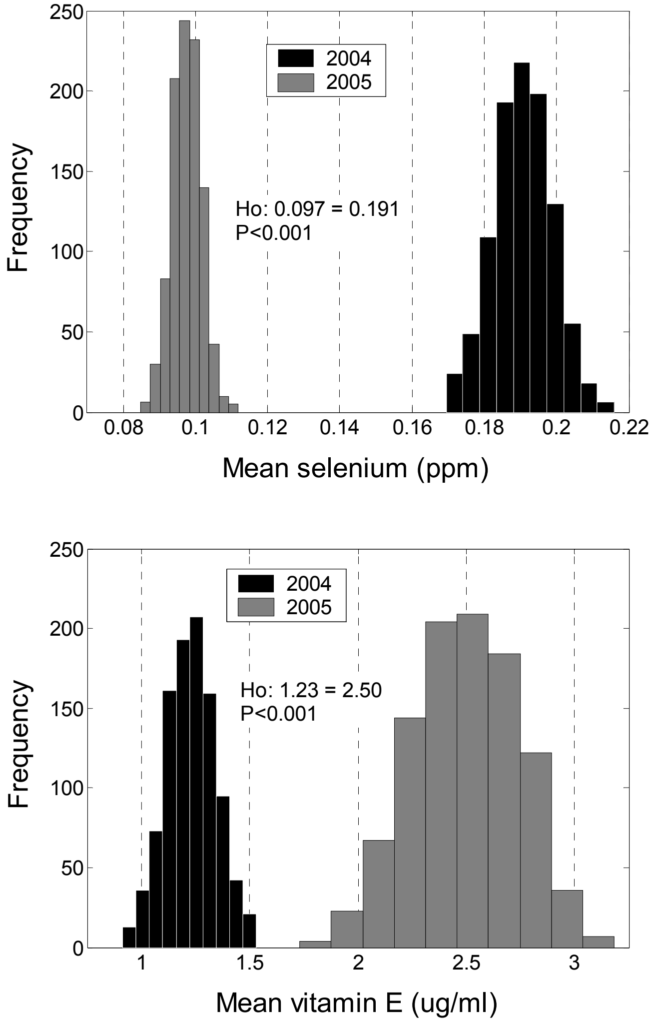

Figure 6.10. Bootstrapped mean distributions of selenium and vitamin E concentrations in sera taken from white-tailed and mule deer in northwest Crockett County, Texas, April 2004 and 2005. P-values are from randomized 2-tailed t-tests for mean differences between years (Manly 2007).

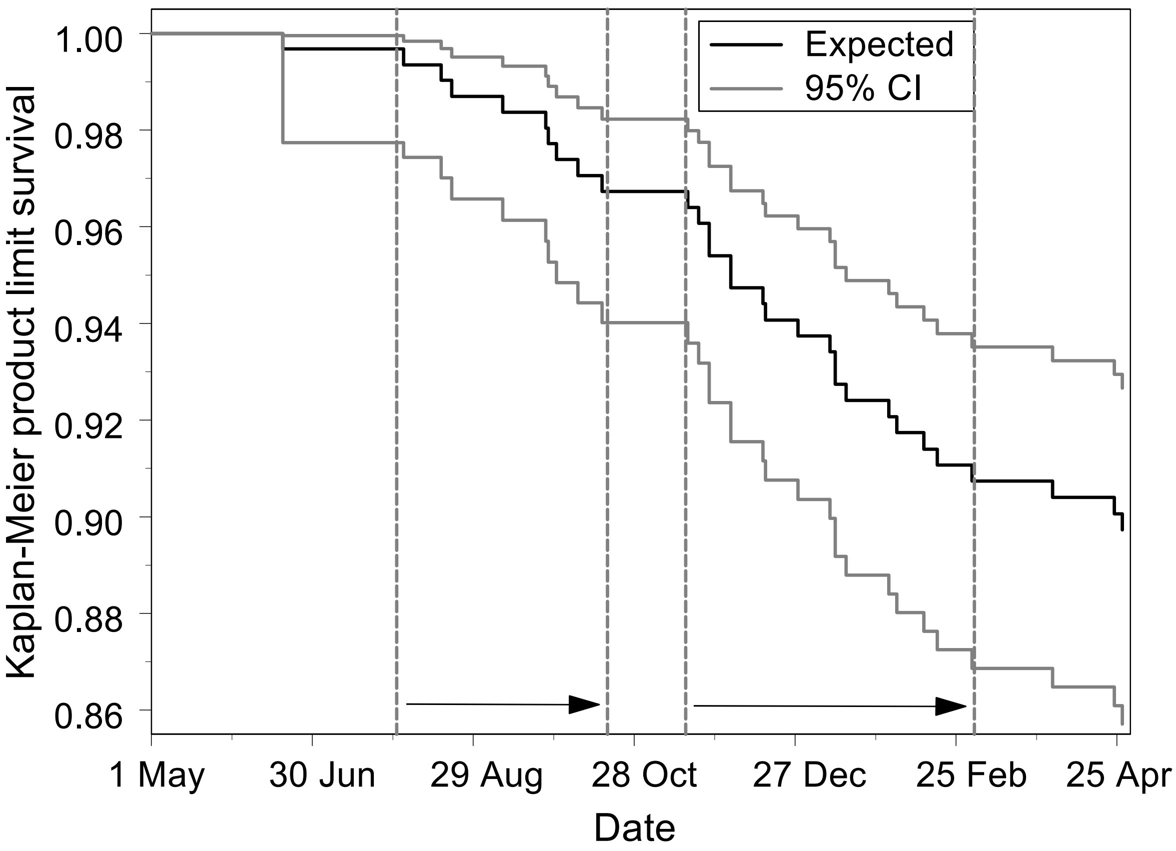

Figure 6.11. Kaplan-Meier survival distribution function for adult female white-tailed and mule deer combined with survival periods starting on 1 May 2000, 2001, and 2004–2006 in northwest Crockett County, Texas. Periods between paired vertical dashed lines may represent periods of reduced survival.

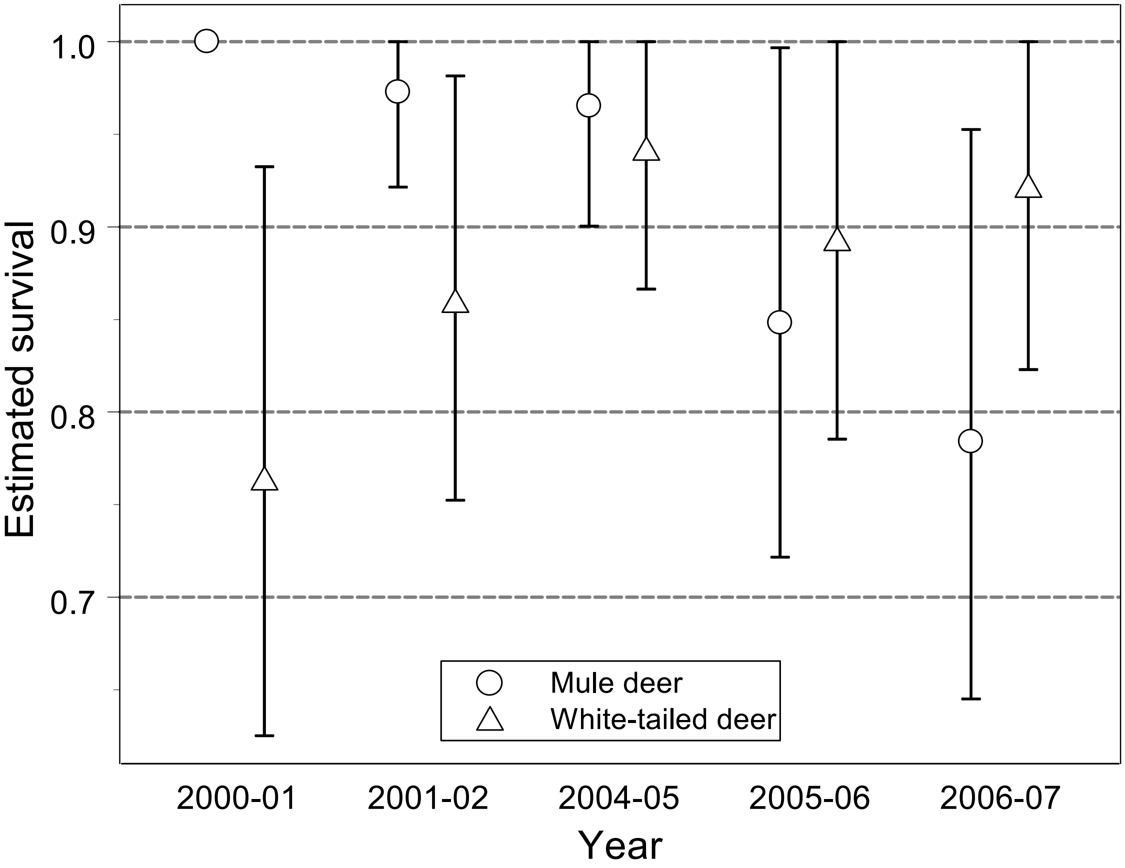

Figure 6.12. Cox regression annual survival estimates (95% CI) of adult female white-tailed and mule deer with survival periods starting on 1 May 2000, 2001, and 2004–2006 in northwest Crockett County, Texas.

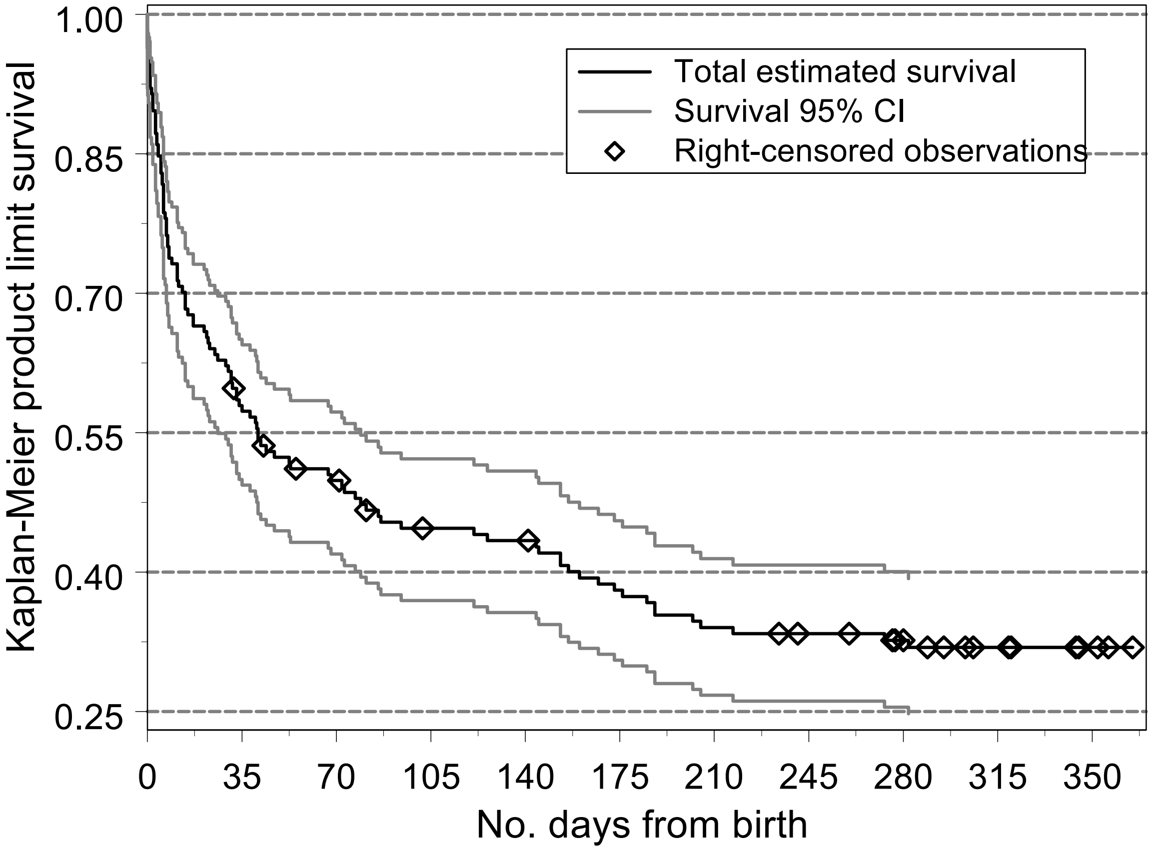

Figure 6.13. Kaplan-Meier survival distribution function for white-tailed and mule deer fawns combined with common entry at individual birthdays during summers 2004–2006 in northwest Crockett County, Texas. One-hundred thirty-nine neonates were from adult females with data histories, and 25 fawns were from unknown adult females. Right-censored fawns from dropped collars or last time heard (*n* = 24) or at 365 days (*n* = 31).

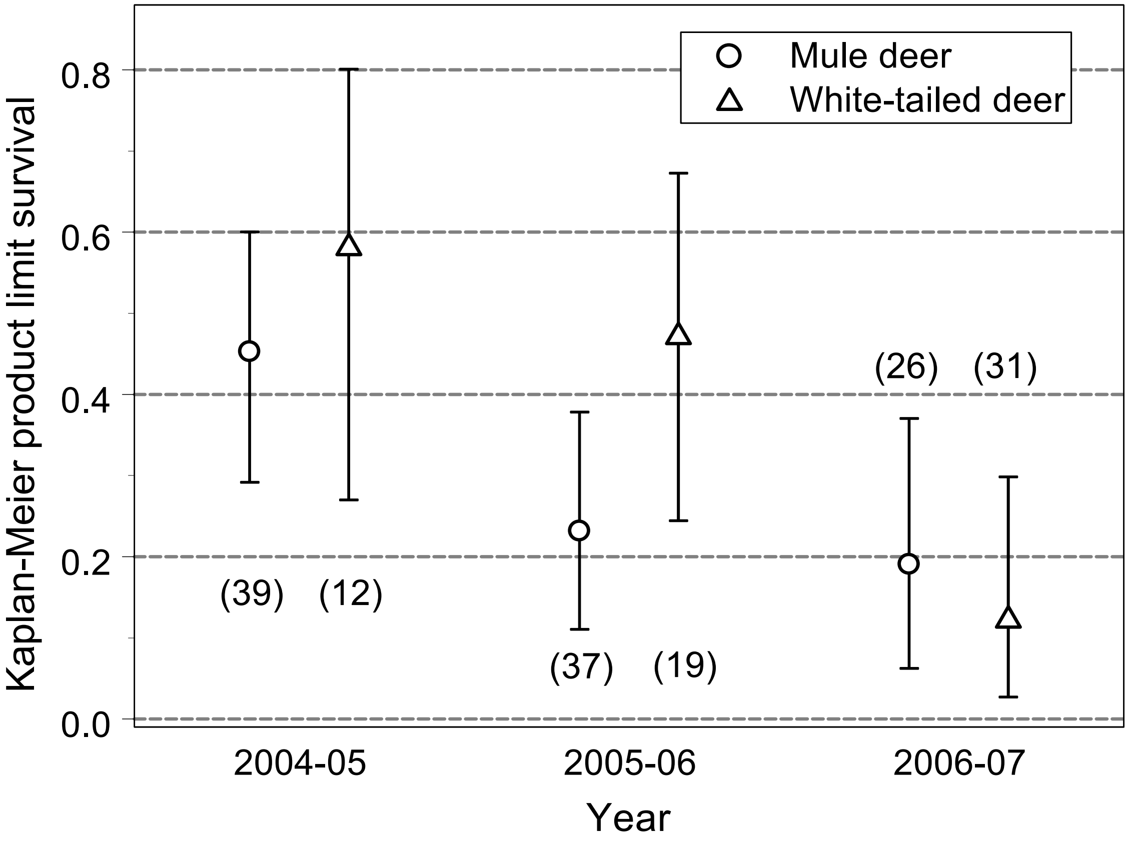

Figure 6.14. Kaplan-Meier annual survival estimates (95% CI) for 164 white-tailed and mule deer fawns captured during summers 2004–2006 in northwest Crockett County, Texas. Number of fawns captured by species and year in parentheses.

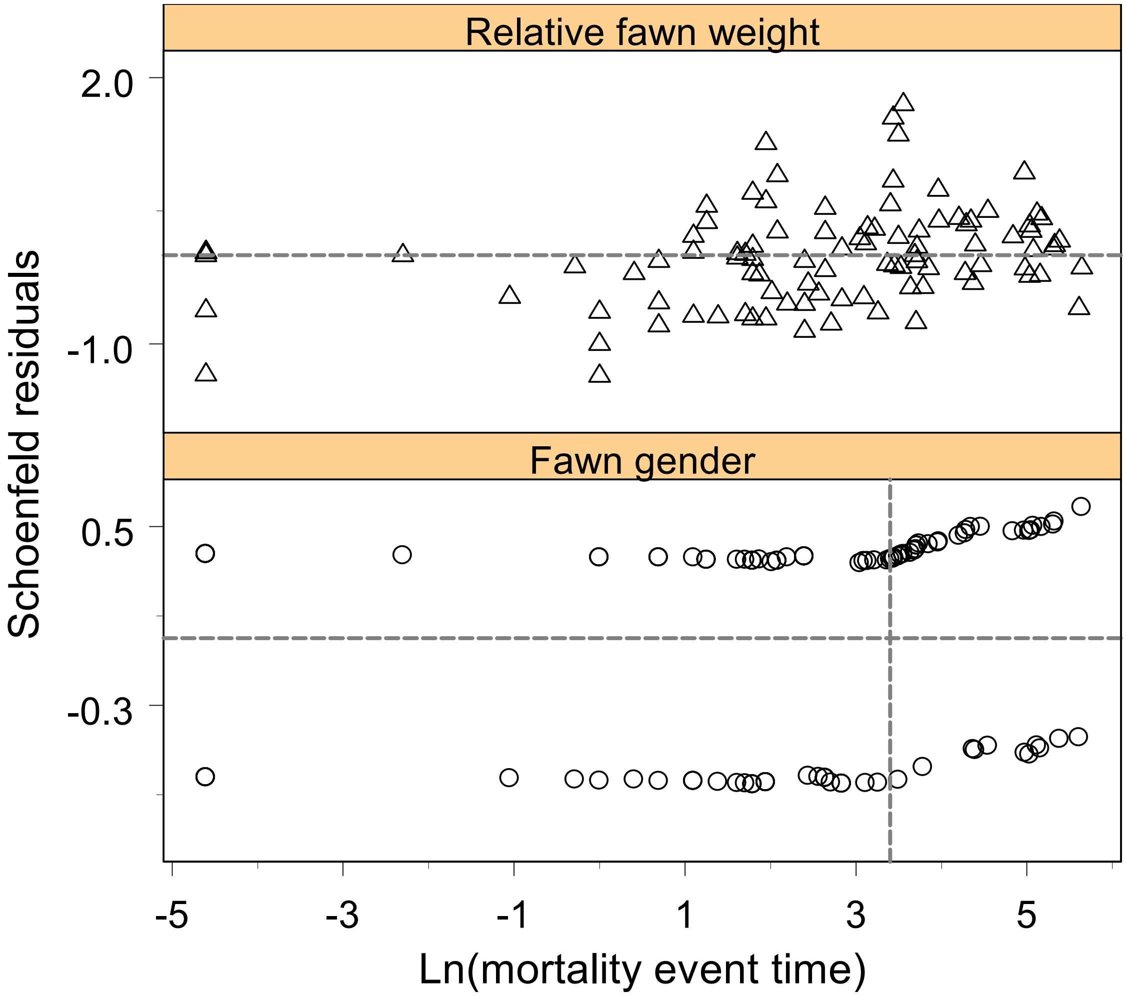

Figure 6.15. Schoenfeld residuals for fawn gender and relative fawn weight versus the natural logarithm of mortality event time (days) for a preferred time-independent model explaining survival of white-tailed and mule deer fawns captured in northwest Crockett County, Texas, summers 2004–2006. Residuals for fawn weight show relatively continuous increase, whereas gender residuals increase after about 30 days (i.e., vertical reference line at ln[30]=3.4). Horizontal lines for zero reference.

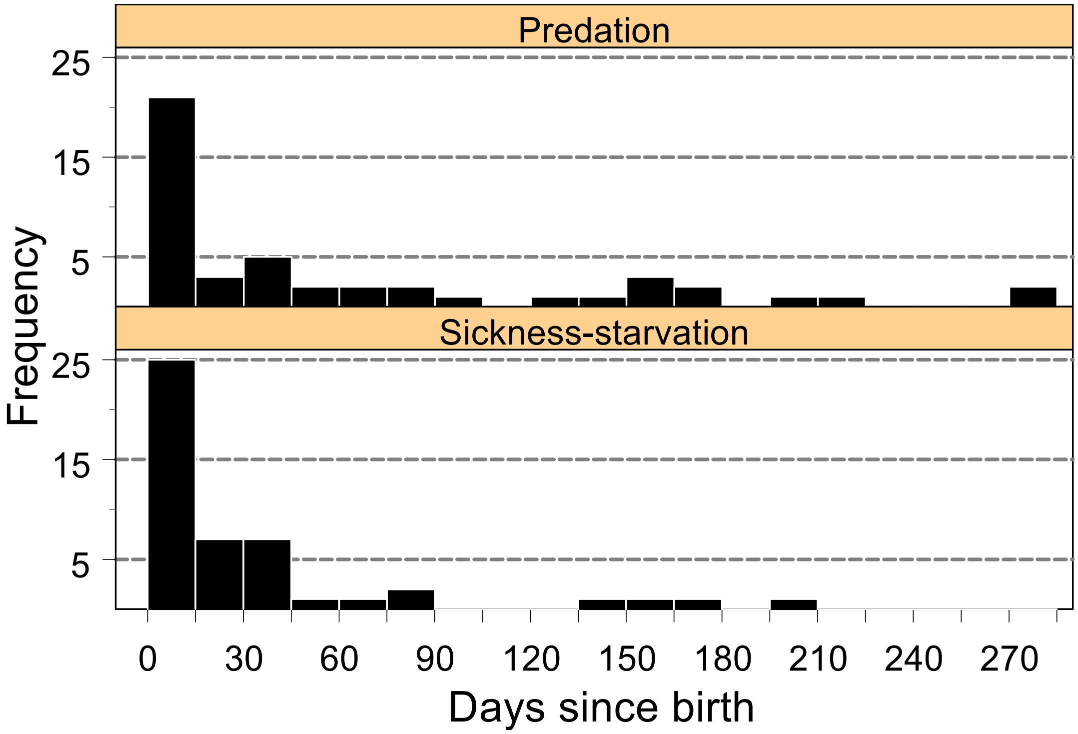

Figure 6.16. Frequency and timing of mortality events by predation and sickness-starvation for 139 white-tailed and mule deer fawns captured from known adult females in northwest Crockett County, Texas, summers 2004–2006.

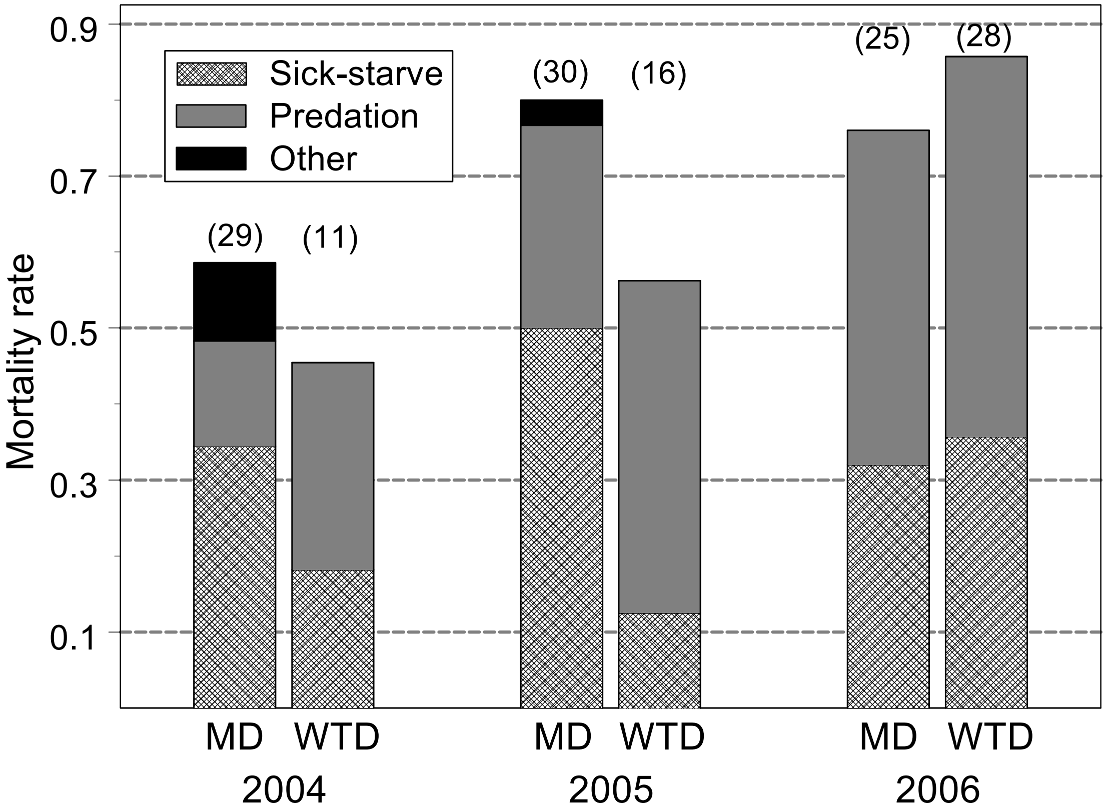

Figure 6.17. Cause-specific mortality rates for 139 white-tailed and mule deer fawns captured from known adult females in northwest Crockett County, Texas, summers 2004–2006. Rates calculated simply as frequency divided by sample size (*n*); 10 fawns right-censored before recruitment date included in samples. Undetermined cause included with other.

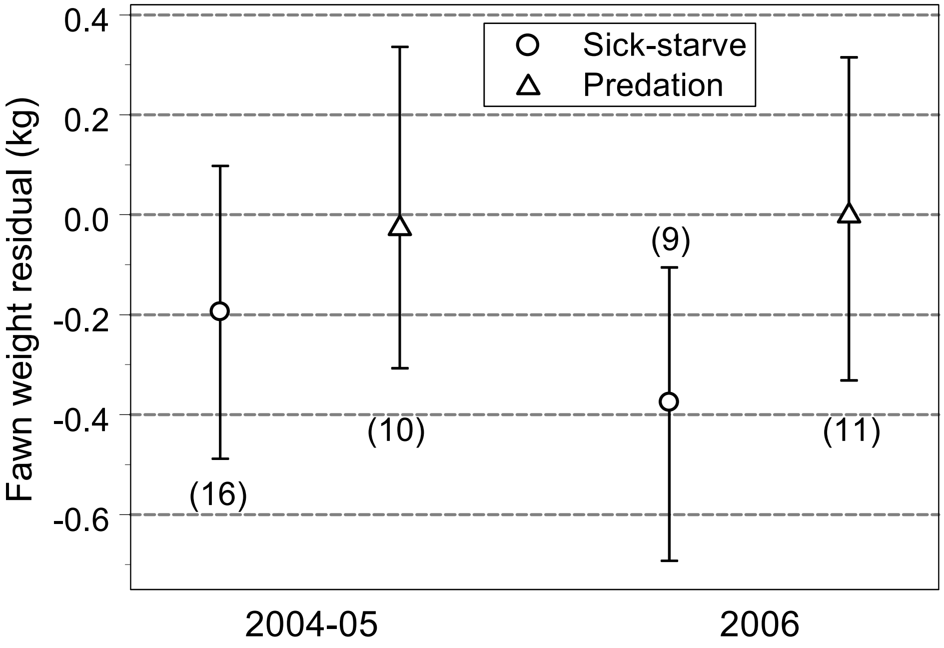

Figure 6.18. Bootstrapped (1000 iterations) mean distributions (95% CIs) of individual residuals from the best fawn weight model (Table 7) for white-tailed and mule deer fawns succumbing to sickness-starvation or predation at ≤15 days-old, northwest Crockett County, Texas, in 2004-2005 and 2006. Sample sizes in parentheses.

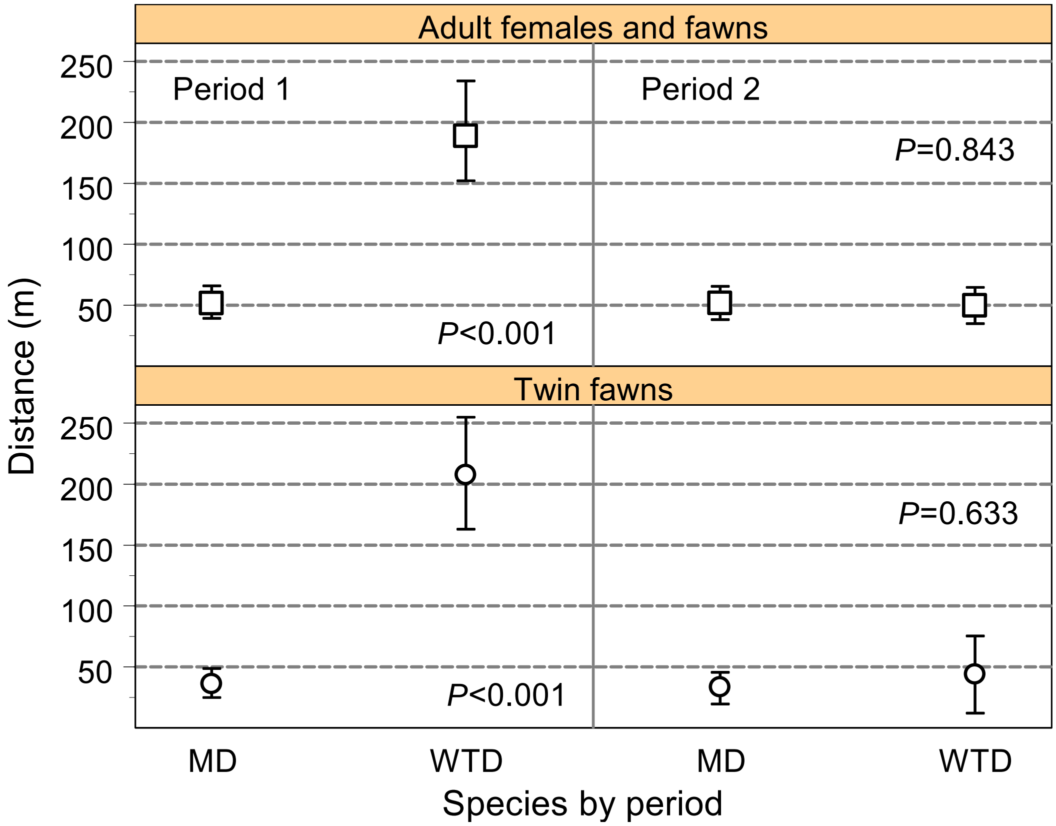

Figure 6.19. Bootstrapped mean distributions (95% CIs) of distances between adult females and concomitant fawns and distances between twin fawns for white-tailed and mule deer in northwest Crockett County, Texas. All mule deer data and most white-tailed deer data from 2004 and 2005 cohorts. Period no. 1 is <3 weeks postpartum during fawns' hider phase, and period no. 2 is >30 days postpartum. For within period comparisons, p-values from randomized t-tests.

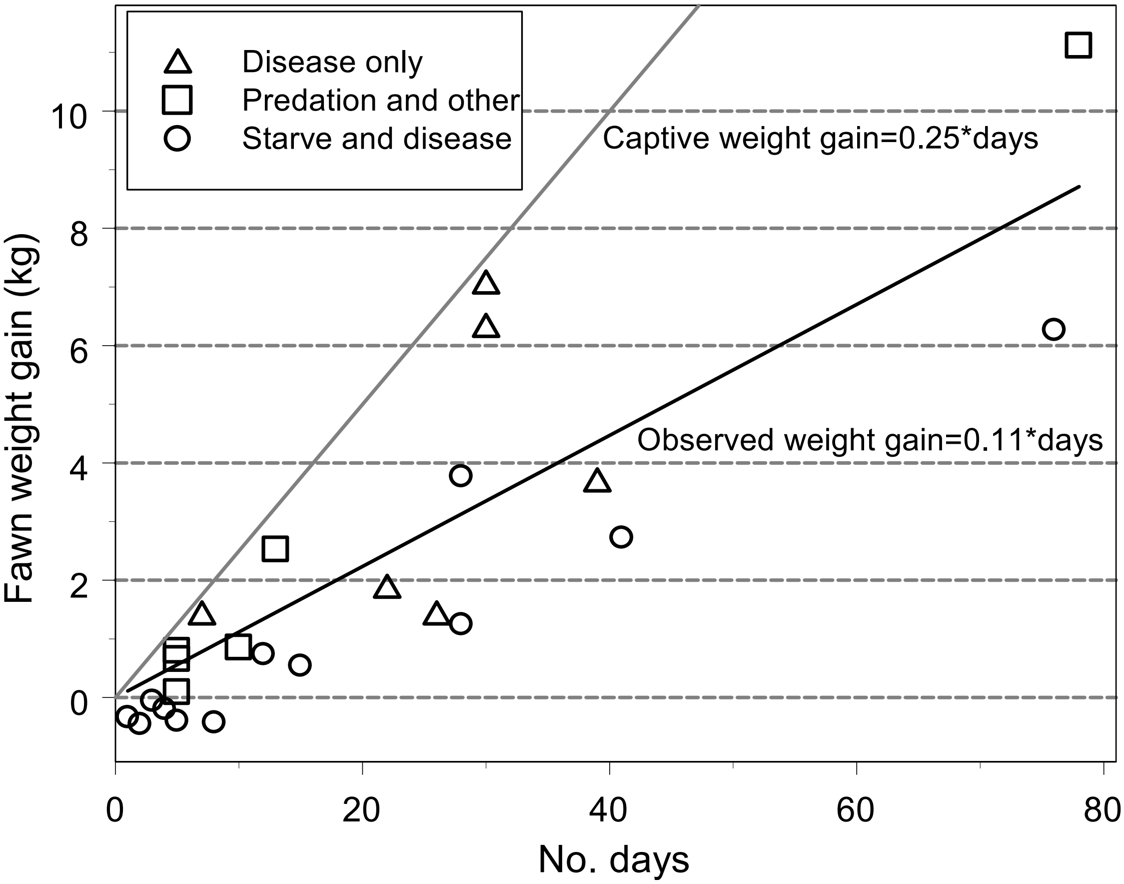

Figure 6.20. Weight gain (kg) of intact white-tailed and mule deer fawn carcasses recovered in Crockett County Texas, 2004–2006. All fawns considered survived >3 days, so were presumed to nurse once. Weight and number of days were differences between capture and death. Causes of death were disease only, predation or 1 other cause, and starvation or starvation and disease combined. Expectation for observed weight gain is linear least squares with zero intercept; expectation for captive fawns from literature (Verme 1963, 1989; Murphy and Coates 1966; Robinette et al. 1973; Thompson et al. 1973; Robbins and Moen 1975).

Appendix A. Fifteen photographs demonstrating clinical signs of fawns succumbing to sickness, starvation, and predation. Speculative diagnoses based on information from Davidson and Nettles (1997), Williams and Barker (2001), and Gaydos (2005). In order of right-to-left and top-to-bottom the photos represent: 1) a fawn born as a mummified fetus typical of bovine viral diarrhea virus infection of the genus *Pestivirus*, 2) a stillborn fawn that received trauma, probably from its dam; the twin was found dead in an acacia bush 20 m from this birth site, 3) a malformed fawn with possible piebald traits but also possibly related to the *Pestivirus*; died in birth site, 4) a typical bobcat kill of a white-tailed fawn, 5) a typical bobcat kill of a mule deer fawn in 2004 and 2005, 6) a fox kill, 7) a knee infection that may have originated as a navel infection of *Staphylococcus* or other bacterium prior to septicemia (R. Sprowls, Texas Veterinary Medical Diagnostic Lab, personal communication); this fawn also starved, 8) purulent viscera possibly of similar origin as no. 7; this fawns also starved, 9) a subcutaneous cranial infection of unfamiliar origin, 10) oral abscesses symptomatic of the historically under-diagnosed adenovirus hemorrhagic disease of *Adenovirus* origin, but buccal necrosis can stem from *Orbivirus* as well , 11) sub-mandibular impaction possibly of similar origin as no. 10, 12) tongue lesions associated with more commonly identified bluetongue or epizootic hemorrhagic disease of *Orbivirus* origins, but also symptomatic of *Adenovirus*, 13) hind-leg subcutaneous hemorrhaging typical of blackleg or malignant edema from anaerobic bacteria of the genus *Clostridium*, 14) a starved singleton fawn that weighed 3.3 kg when captured at <1 day-old and 6.0 kg when recovered at 41 days-old (Appendix B), and 15) 144 day-old fawn with hind legs crusted with diarrhea possibly associated with salmonellosis of *Salmonella* bacterium or

Appendix A. continued

Escherichia coli (Kramer et al. 1971). Photos 1, 3, 4, 6, 7, and 12 were white-tailed fawns; others were mule deer. The photos shown were representative of other cases and some but not all pathogens possibly present. Other informative photos and potential pathogens not included were: 1) a possible case of anthrax by the bacterium *Bacillus anthracis*, in which case we did not perform a necropsy, 2) possible dermatophilosis from the bacterium *Dermatophilus congolensis*, 3) fawns with clouded eyes that may have been symptomatic of malignant catarrhal fever of *Herpesvirus* origin with domestic sheep as a typical vector 4) a non-marked fawn (not included in analyses) found dead and entangled in the mesh fence typical of this area; we had no fence mortalities in marked fawns, 5) the rumen of an adult mule deer female impacted with 2 bowling ball-sized boluses of coarse juniper forage; many papillae were eroded or missing which is a typical sign of chronic hemorrhagic disease of both *Orbivirus* and *Adenovirus* origin; she also had an impacted oral abscess, and 6) possible leptospirosis by the spirochete bacterium *Leptospira interrogans* evidenced by a vaginal infection in an adult mule deer that was barren in April 2006 and succumbed later that year.















Appendix B. Incidence of known weaning (i.e., presence of milk curds in stomach; N=no, Y=yes) and fawn age at death (days) for white-tailed and mule deer fawns captured in northwest Crockett County, Texas, 2004–2006. Potential explanatory variables included ranch location (N=north, S=south), species (M=mule deer, Wt=white-tailed deer), gender (F=female, M=male), mortality type (O=other, P=predation, SS=sickness-starvation), and year as it may relate to rain duirng late-gestation and lactation (Fig. 5).

Fawn ID	Weaned	Fawn age[a]	Ranch location	Species	Gender	Mortality type	Year
F11H	N	1.5	N	Wt	F	SS	2006
F17E	N	2	N	M	M	SS	2005
F11G	N	3	N	Wt	F	SS	2006
F52A	N	3	N	M	M	SS	2004
F35H	N	4	N	M	F	SS	2006
F16D	N	5	N	M	F	P	2005
F44B	N	6.5	N	M	M	O	2004
F45D	N	7	N	M	F	P	2005
F01B	N	7.5	N	M	M	SS	2004
F21D	N	8	N	Wt	M	SS	2005
F60G	N	11.5	N	Wt	F	P	2006
F04H	N	14	N	M	F	P	2006
F37A	N	31	S	M	M	SS	2004
F44A	N	31.5	N	M	M	SS	2004
F37G	N	40	S	M	M	SS	2006

Appendix B. Continued

F68E	Y	4	S	M	M	SS	2005
F37B	Y	5	S	M	M	SS	2004
F69D	Y	5	S	M	F	SS	2005
F93G	Y	7.5	S	M	F	SS	2006
F11D	Y	9	N	Wt	M	P	2005
F27E	Y	15	S	M	F	SS	2005
F49D	Y	15.5	S	M	M	P	2005
F49H	Y	17	S	M	F	SS	2006
F37C	Y	29	S	M	M	SS	2004
F19A	Y	33	S	Wt	M	SS	2004
F25A	Y	41	S	M	M	SS	2004
F29G	Y	53	S	Wt	M	SS	2006
F71D	Y	68	N	M	M	SS	2005
F41E	Y	72	N	M	M	P	2005
F43B	Y	77	S	M	M	SS	2004
F54B	Y	121	N	M	M	P	2004
F43E	Y	145	S	M	F	P	2005
F34H	Y	156	N	M	M	SS	2006
F25E	Y	176	S	M	M	SS	2005
F64D	Y	185	N	Wt	M	P	2005
F55A	Y	188	N	M	F	P	2004
F36G	Y	282	S	Wt	M	P	2006

[a] Fawns >60 days-old not considered for initial regression modeling