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

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During a study of fawn mortality, 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 to 2006. We treated this aspect of the 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: within-year variation among individuals within species, because older and heavier females gave birth earlier; among-year variation at the population level, because greater rain during the previous prerut and rut periods resulted in earlier birth dates; and a chronic-cohort effect also at the population level, because even after previous effects were accounted for in regression models, deer gave birth later on more intensely grazed ranches. After accounting for mass, age of females 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 sex or rain during gestation. Overall, Kaplan–Meier product-limit estimates indicated that birthing by white-tailed deer peaked on 20 June (90% range = 31 days) and birthing by mule deer peaked on 21 July (90% range = 45 days). We suggest that the 1-month separation between peak birth dates and breeding periods of these sympatric species of deer was partly due to 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*, overgrazing, population, proximate factors, rain, sympatry, Texas

Reproductive aspects of ungulate biology have been examined from an evolutionarily adaptive viewpoint (Caley and Nudds 1987; Ims 1990; Rutberg 1987; Sheldon and West 2004; Verme 1983). Resource pulses related to the effects of local climate on vegetative phenology can explain timing and synchrony of birthing seasons (Côté and Festa-Bianchet 2001; Gogan et al. 2005; Loe et al. 2005; Post et al. 2003; Sinclair et al. 2000), especially for species with hiding neonates such as those of *Odocoileus* (Geist 1998; Lent 1974; Rutberg 1987). In north-temperate species, there often exists a trade-off between timing parturition to coincide with plant emergence and constraints imposed by the short growing season before onset of breeding and winter (Cook et al. 2004; Gaillard et al. 1993; Langvatn et al. 2004). Researchers have found considerable plasticity in birth seasons at subfamilial levels (Clutton-Brock and Harvey 1984; Hass 1997; Rachlow and Bowyer 1994; Rutberg 1987) as well as some degree of phylogenetic constraint relative to variability in local environments where the species is native or introduced (Asher et al. 1999; Bowyer et al. 1998; Hass 1997; 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 parturition (Robinette et al. 1973). Poor nutrition during gestation can delay parturition (Nilsen et al. 2004; Verme 1965). Condition indices (e.g., body mass and thickness of rump fat) measured pre- and postpartum may be correlated

with breeding condition and have been negatively correlated with date of birth (Birgersson and Ekvall 1997; Cameron et al. 1993; Keech et al. 2000). Poor nutrition in the summer–autumn prerut and rut periods can be related to climatic conditions and can delay estrus, breeding, and parturition (Adams and Dale 1998; Cook et al. 2001, 2004; Verme 1965). 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 give birth earlier than those of lower status, regardless of the sex of their offspring (Guilhelm et al. 2002; Holand et al. 2004b; San Jose et al. 1999).

Published results regarding sex of offspring are more conflicting. Some accounts suggest that early breeding and birthing by deer were associated with a predominance of male offspring (Hemmer 2006; Holand et al. 2006). Sex of offspring may be affected by the male parent, with dominant male cervids in polygynous species breeding early and siring more males (Gomendio et al. 2006; Roed et al. 2007). However, birth dates may not accurately reflect breeding dates because of variable and possibly compensating gestation lengths (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 females and produced mostly male fawns, whereas older females "under the best nutritional circumstances" conceived more female offspring (Dapson et al. 1979; Ozoga and Verme 1982:281; Verme 1981). Another study of captive white-tailed deer reported conception dates unrelated to sex of offspring (DeYoung et al. 2004).

Last, populations with low abundance of adult males may exhibit later birth dates, presumably because females do not find suitable mates during their 1st estrus (Holand et al. 2003; Komers et al. 1999; Saether et al. 2003). Also, it may be important to consider that individual or cohort differences among female offspring such as mass, dominance, and reproductive characteristics may persist through adulthood and may be passed to the next generation (Gaillard et al. 2000, 2003; Garroway and Broders 2005; Guilhelm et al. 2002; Hewison et al. 2005; Mech et al. 1991).

Our objective was to assess which aforementioned factors might have influenced parturition or breeding dates of sympatric deer on private lands in west-central Texas from 2004 to 2006, a period with considerable variation in precipitation patterns. Before our study, we understood that white-tailed deer probably gave birth earlier than mule deer (M. Humphrey, in litt.). We present a case in which neonates were captured from free-ranging females with known histories, so we were able to model individual- as well as population-level effects. Body mass, fatness, and age may be good indicators of social status of adult females as well as individual condition (Holand et al. 2004a; Veiberg et al. 2004; Vervaecke et al. 2005). For most fawns captured, we had measures of all 3 variables that were somewhat correlated with one another. We considered potential population-level effects of precipitation during the prerut–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 give 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, male:female ratios were consistent at 1 male per 2.5 females, and pregnancy rates were high (S. Haskell, in litt.).

MATERIALS AND METHODS

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 semiarid transition zone between the Great Plains and Southwest Deserts ecoregions. Elevations ranged from 870 m above sea level on mesa tops to 750 m above sea level 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/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 2-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 individuals/km^2 in autumn 2005 (Haskell et al., in press). The male:female ratio was about 1:2.5 (Haskell et al., in press). 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).

Field methods.—In April 2004–2006, we captured adult female deer using a net-gun fired from a helicopter (Holt Helicopters, Uvalde, Texas; Krausman et al. 1985). We weighed each deer with a Hanson hanging scale (Hanson, Northbrook, Illinois) and pulled a tooth for aging by cementum annuli after administering lidocaine as a local anesthetic (Matson's Laboratory, Milltown, Montana; Mansfield et al. 2006; Swift et al. 2002). 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 female with a vaginal-implant transmitter (ATS, Isanti, Minnesota) and radiocollar (Telonics, Mesa, Arizona, and ATS). The vaginal-implant transmitters were used to help locate neonates for capture <24 h after birth
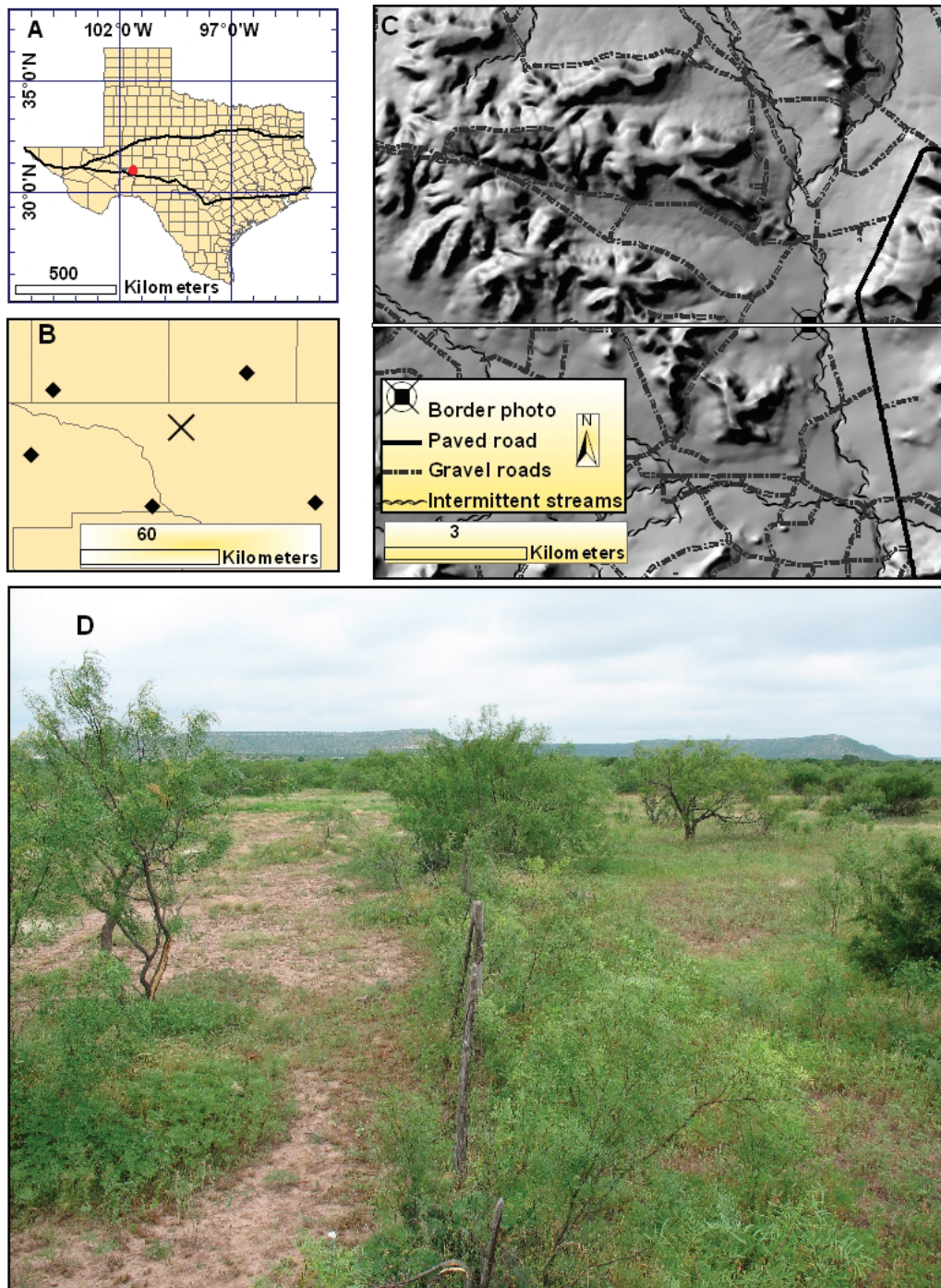
FIG. 1.—Site for study of sympatric white-tailed and desert mule deer in west-central Texas, 2004–2006, including: A) location in northwest Crockett County near interstate highway 10, B) location of 5 NOAA weather stations around the study area, C) shaded relief of the study area with horizontal line delineating north ranches from south ranches, and D) north–south fence-line photo taken on 29 June 2007 from east to west. South ranch was more intensively grazed than north ranch.

(Carstensen et al. 2003). We used the precise-event codes from vaginal-implant transmitters, information from monitoring schedules, and evidence from birth-sites to estimate time of births within 0.5–10 h (Haskell et al. 2007). We also captured fawns opportunistically; age of these fawns was determined 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, and met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

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
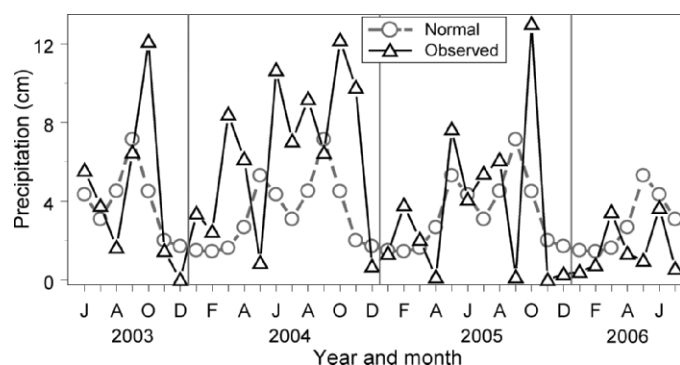
FIG. 2.—Monthly precipitation patterns averaged from 5 NOAA weather stations located at Big Lake, Ozona, Sheffield, Bakersfield, and McCamey, Texas, 2003–2006, compared to average normal precipitation. Precipitation was nearly 100% as rain. Vertical lines delineate years.

center of our study site (NOAA National Climatic Data Center, Asheville, North Carolina). 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, because rainfall in this region can often be localized. We summed the monthly averages from August–December 2003–2005 to represent the prerut 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 in recent years (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 to 1.6 m above the ground in similar mesquite (*Prosopis glandulosa*)–tarbush (*Flourensia cernua*) habitats ($t = 2.44$, $d.f. = 102$, $P = 0.017$; D. Butler, in litt.). Thus, we hypothesized that even after annual variability in individual- and population-level effects were accounted for in regression models that a chronic intergenerational 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 before mid-May. Therefore, our data set 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 females among years. We entered each twin into the data set independently because it was necessary to do so to examine a potential effect of sex on birth dates, and occurrence of twins appeared unrelated to birth date; most fawns were in sets of twins regardless. Also, capturing fawns from the same females 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; Kleinbaum and Klein 2005). Thus, we tried to account for potential family effects using PROC NLMIXED (SAS Institute Inc. 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 before 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 assess 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). Mass of females 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 mass of females by AIC corrected for small sample size (AIC_c). We plotted Kaplan–Meier cumulative survivorship curves using SAS PROC LIFETEST and S-Plus 7.0 (Insightful Corp., Seattle, Washington) to help describe categorical covariate effects (Fox 2001; Kleinbaum and Klein 2005).

TABLE 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 sex (2), location (3), cumulative rain from August–December of the previous year (4), cumulative rain from January–May (5), age of females (6), mass of females (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 (log L, number of estimated parameters (K), and model selection by information-theoretics (AIC).[a]

Model	Parameter(s)	R^2_{LR}	Log L	K	AIC	AIC_c	ΔAIC_c	ω_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

[a] AIC = Akaike information criterion; AIC_c = Akaike information criterion corrected for small sample size; ω_i = Akaike weight.

RESULTS

In each April 2004–2006 we captured and fitted 25 females of each species with vaginal-implant transmitters; in 2005 and 2006 we recaptured surviving females and replaced dead deer ($n = 1$ and 9, respectively). All females were pregnant in 2004 and 2005, and 2 adult mule deer and 1 yearling white-tailed deer 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, because 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 females. Of these 163 fawns, only 138 were captured from 54 separate females with known data histories including age and body weight at capture in April. An additional 2 fawns were from 2 marked females that were missing data on body fat. We captured 25 fawns from 21 females that were not marked or handled by researchers, so we were unable to include these observations in any model considering individual characteristics of females. Overall, Kaplan–Meier product-limit estimates indicated that parturition by white-tailed deer peaked on 20 June with 90% occurring within 31 days and parturition by mule deer 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 versus south), August–December precipitation, January–May precipitation, age of females, and mass of females 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 ($\chi^2 = 1.29$, $d.f. = 1$, $P = 0.258$), sex ($\chi^2 = 1.14$, $d.f. = 1$, $P = 0.287$),

January–May precipitation ($\chi^2 = 1.31$, $d.f. = 1$, $P = 0.253$), mass of females ($\chi^2 = 5.53$, $d.f. = 1$, $P = 0.019$), age of females ($\chi^2 = 9.38$, $d.f. = 1$, $P = 0.002$), location ($\chi^2 = 10.55$, $d.f. = 1$, $P = 0.001$), August–December precipitation ($\chi^2 = 15.78$, $d.f. = 1$, $P \leq 0.001$), and finally, species ($\chi^2 = 280.19$, $d.f. = 1$, $P \leq 0.001$).

Consistent with the preceding information, model selection by AIC_c suggested that the model including mass of females 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 2 (Table 1), and the issue of dependence in our data, we suggest that the 2nd most plausible model should be simpler and not more complex. Model 5 (Table 1) would be the 2nd most plausible model after removing mass of females from model 1 (Tables 1 and 2). All other models seemed relatively implausible. Substituting fatness of females for mass of females in model 1 (Table 1) indicated that fatness of females was not com-

TABLE 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 versus south ranches), cumulative rain from August to December of the previous year (cm), age of females at conception (years), and mass of females at capture during gestation in April (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 (SEs), 95% confidence limits (LCL = lower confidence limit; UCL = upper confidence limit), chi-square test value (χ^2, $d.f. = 1$), and P-value. For predictions with this log-linked model, effects must be summed before being exponentiated with 14 May = 0.

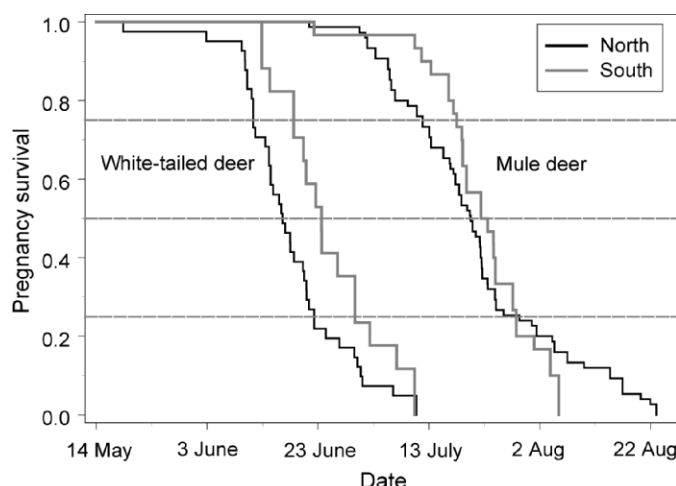| Parameter	Estimate	SE	LCL	UCL	χ^2	$Pr > \chi^2$
Intercept	4.351	0.189	3.982	4.720	533.03	≤0.001
Species	0.698	0.041	0.618	0.779	289.05	≤0.001
Location	−0.124	0.034	−0.189	−0.058	13.71	≤0.001
August−December rainfall	−0.006	0.002	−0.010	−0.003	10.76	0.001
Age of females	−0.028	0.008	−0.044	−0.012	11.91	0.001
Mass of females	−0.009	0.004	−0.016	−0.001	5.53	0.019

FIG. 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.

petitive ($\chi^2 = 0.07$, $d.f. = 1$, $P = 0.792$) even though somewhat correlated with mass of females. The preferred model (Table 1, model 1) indicated that mule deer gave birth later than white-tailed deer, cumulative rain from the previous August–December was negatively related to birth date, older and heavier females gave birth earlier, and 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 age of females and mass of females (Table 1, model 1), population-level effects were species, location, and August–December rain. Although 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% confidence interval [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 to 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. Before 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 a medium amount of January–May rainfall among years. The data on rainfall in January–May during gestation did not fit the data on birthing period well.
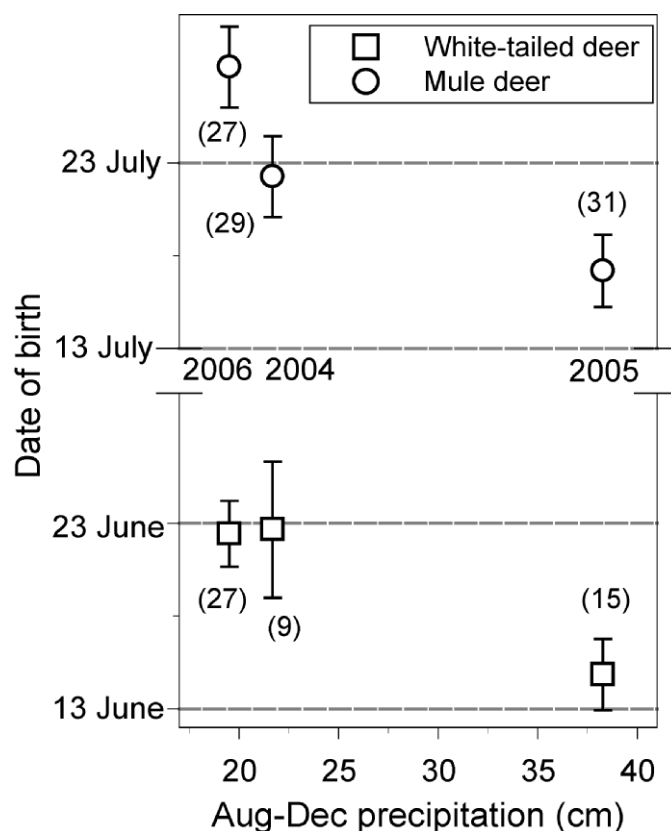

FIG. 4.—Kaplan–Meier product-limit mean estimates (± 1 SE) of white-tailed and mule deer birth dates in 2004–2006 influenced by cumulative precipitation from August–December of the previous year. Year labels correspond to summer birthing periods. Sample sizes in parentheses. Horizontal dashed lines for y axis reference and note y axis break; above and below scaled identically.

DISCUSSION

We examined factors influencing birth dates of deer at 3 hierarchal levels: within-year variation among individuals within species, among-year variation at the population level, and a chronic intergenerational 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 and 2). After controlling for species, the factors influencing birth dates of deer at the same 3 respective hierarchal levels were age and mass of females, cumulative rain during the prerut and rut periods from August–December of the previous year, and 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 (Baker and Bradley 2006; Cronin 2003). 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 due to habitat segregation before mating related to predation risk or

to selection against F_1 hybrids that experienced reduced fitness because of confused subsequent antipredator 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, pers. comm.). 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 parturition dates of white-tailed deer, and presumably breeding, occurred within 31 days at our site. Studies of nearby allopatric populations of white-tailed deer in central and southern Texas indicated that 90% of conceptions occurred within about a 1.5-month period (Harwell and Barron 1975; Teer et al. 1965). 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, although 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% of parturitions occurring within 45 days overall and also exhibiting larger tails in the distribution of birth dates, particularly on the northern ranches with greater relative abundance and interspersion of mesa habitats (Figs. 1C and 3).

We suggest that the difference in mean birthing periods between species was more likely due to some degree of phylogenetic constraint, because both species appeared to be synchronized with parent populations. Mule deer at our site were of the subspecies *eremicus*, adapted to the environments and precipitation regimes of the semiarid and arid southwestern United States. Southwestern deer such as *O. h. eremicus*, *O. v. couesi*, and *O. v. carminis* tend to give birth during July and August in synchrony with summer rains from convective storms (reviewed 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; Van Auken 2000; Wiggers and Beasom 1986). In southern Illinois and central Texas, allopatric populations of white-tailed deer had peak birthing periods near mid-June (Nelson and Woolf 1985; Teer et al. 1965). Thus, although 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 body mass of individual females was accounted for in the regression model, age of females was still a significant factor (Tables 1 and 2). It is well understood that females in better condition may enter estrus, breed, and give birth earlier than those in poorer condition (Adams and Dale 1998; Cook et al. 2001, 2004; Robinette et al. 1973; Verme 1965), 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; Guilhelm et al. 2002; Holand et al. 2004b; Langvatn et al. 2004; San Jose et al. 1999). Regardless of mass, age of females 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 (DeYoung et al. 2006; Geist 1981; Hoem et al. 2007; Johnson et al. 2007; Marchinton and Hirth 1984), but such behavior can occur among females as well (Bergerud 1974). Côté and Festa-Bianchet (2001) found no effects of maternal age or social rank on birth dates of mountain goats (*Oreamnos americanus*), 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 male deer 1st tended older and mature females that exhibited dominance over younger females, and that younger subordinate females delayed their 1st estrus until a few days after that of dominant females to obtain fawn-rearing advantages related to postpartum behavior or predator swamping (Aycrigg and Porter 1997; Nixon and Etter 1995; Ozoga and Verme 1986; Ozoga et al. 1982; Whittaker and Lindzey 1999). Alternatively, behavioral interference may have caused some young deer to remain barren after their 1st estrus. Such hypotheses are difficult to test under free-ranging conditions, but our data were suggestive of a behavioral effect associated with age of females.

Similar to McGinnes and Downing (1977), we found that population-level environmental influences on birth dates operated before conception and not during gestation. Cumulative rainfall during the prerut 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 data on rainfall for December from the relationship to birth dates of white-tailed deer would have no real effect on a similar analysis (Fig. 2), but removing the data for August from the analysis of mule deer would cause a relative increase of total rainfall in 2003 and improve the fit of the data (Fig. 4). McGinnes and Downing (1977) found delayed parturition after relatively high survival of fawns from the previous year, presumably because energetic demands of lactation on females successfully rearing fawns may result in relatively poor condition and delayed breeding in autumn. However, from 2004 to 2006, our population of deer experienced greatest recruitment of fawns from the 2004 cohort before the earliest birthing period in 2005 (Fig. 4; S. Haskell, in litt.). Thus, deer at our site may invest less energy rearing fawns and seemed more influenced by variability in rainfall occurring before conception.

Land-use practices that alter behavior and patterns of resource use by wildlife may or may not affect population parameters (Cronin et al. 1998; Mallord et al. 2007). On average, deer on the northern ranches gave birth earlier than those on the southern ranches (Fig. 3; Tables 1 and 2). After accounting for individual- and population-level variability within and among years (Table 2), this remaining effect may be related to more intensive grazing 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 intergenerational or cohort effects are known (Gaillard et al. 2000, 2003; Garroway and Broders 2005; Guilhelm et al. 2002; Hewison et al. 2005; Mech et al. 1991). Also, contiguous deer populations have previously demonstrated different demographics due to localized relationships to vegetative carrying capacities (Dapson et al. 1979). 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 are substantially larger than the home ranges of deer, it is plausible that demographics could differ across a fence-line (Fig. 1D). It is not known if vital rates such as production and survival of fawns were also altered by these land-use differences (e.g., Hailey et al. 1966; McMahan 1964; McMahan and Ramsey 1965; Taylor and Hahn 1947), 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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