ACTIVITY OF DESERT MULE DEER DURING THE BREEDING SEASON

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Motion-sensitive radiocollars and an automated telemetry system were used to quantify relative activity levels of desert mule deer (*Odocoileus hemionus crooki*) in southwestern Texas during the 1990–1991 breeding season. Activity data were divided into prerut, peak rut, and postrut periods and analyzed for gender and period effects. Gender did not affect relative activity level, and activity increased from prerut to peak rut to postrut. Of four possible explanations for the increased activity from prerut to postrut (day length, mate searching, increased feeding, and shifted breeding season), mate searching was supported best by the results.

Key words: mule deer, *Odocoileus hemionus,* Texas, breeding, activity

Patterns of animal activity offer insight into how animals allocate their energy through time. For desert mule deer (*Odocoileus hemionus crooki*), activity during the breeding season is energetically demanding and likely is linked to the increased mortality that follows breeding (S. Demarais et al., in litt.). In addition, the breeding season in many states coincides with the harvest season. Thus, it is the applied ecologist's challenge to understand how changes in activity and behavior may influence natural and human-induced mortality and what the effect may be on the population. Quantifying changes in deer activity and behavior and explaining the causes should help provide this understanding.

Activity patterns of ungulates have been studied for annual and seasonal patterns in moose (*Alces alces*—Renecker and Hudson, 1989), elk (*Cervus elaphus*—Craighead et al., 1973; Georgii, 1981), white-tailed deer (*Odocoileus virginianus*—Cohen et al., 1989), and mule deer (*O. hemionus*—Dasmann and Taber, 1956; Eberhardt et al., 1984; Kufeld et al., 1988). However, we found only two studies that quantified behavioral changes within the breeding season, and these were on white-tailed deer (Holzenbien and Schwede, 1989; Ozoga and Verme, 1975).

Ungulate activity has been measured in various ways. Michael (1970) and Miller (1970) used the number of deer observed per hour as an index of activity. Tracks per day defined activity for Ockenfels and Bissonette (1984). Kammermeyer and Marchinton (1977) used linear distances between relocation points divided by the elapsed time. Spotlight counts were used by Newhouse (1973), whereas the percentage of active deer on such counts was used by McCullough (1982). More recent studies have used telemetric methods. Beier and McCullough (1990) used mercury tip-switch collars that indicated head-up or head-down positions; scans consisting entirely of one position were used to indicate an inactive animal, and the percentage of the day spent active was calculated. Our objective was to quantify behavioral patterns using radiocollars with continuously variable motion sensors to record relative activity during the breeding season. These radiocollars allowed us to determine differences in activity levels between genders, among three breeding periods, and among 12 2-h intervals of the day.

Materials and Methods

The research was conducted on Elephant Mountain Wildlife Management Area and surrounding private ranches (ca. 16,000 ha) in Brewster Co., 42 km S Alpine, Texas. The climate was semiarid with annual rainfall averaging 34 cm. Most precipitation fell from May to September, with mean temperature highs of 32°C and lows of 13°C. The October-to-April dry season had mean temperature highs of 31°C and lows of 0°C (United States Department of Commerce, 1990, 1991). Elevation ranged from 1,300 to 1,900 m, and topography included wide valleys, rugged mountains, and deep canyons. The research area was a Chihuahuan Desert shrub community. Woody vegetation included honey mesquite (*Prosopis glandulosa*), creosotebush (*Larrea tridentata*), tarbush (*Flourensia cernua*), redberry juniper (*Juniperus pinchotii*), piñon pine (*Pinus cembroides* and *P. edulis*), and areas of oak (*Quercus*) near ephemeral water sources. Xeric sites had lechugilla (*Agave lechugilla*), cholla (*Opuntia imbricata*), ocotillo (*Founquieria splendens*), and yucca (*Yucca*). Common grasses included alkali sacaton (*Sporobolus airoides*), silver bluestem (*Bothriochloa saccharoides*), grama (*Bouteloua*), and threeawn (*Aristida*—Correll and Johnston, 1979).

Thirty-four yearling and adult mule deer (22 males and 12 females) were captured and radiocollared during February–March 1990 using drop-nets and net-guns. The deer were captured 8 months prior to monitoring of activity as part of a larger study. Each animal was fitted with a radiocollar containing two motion sensors, one for quantifying activity and one for detecting mortality (Advanced Telemetry Systems, Isanti, MN). The activity sensor linearly increased the number of pulses added to the base rate of the transmitter as collar movement increased. Extra room was provided on collars for males for swelling of the neck during the rut, and the battery case of each radiocollar was painted in a color pattern to supplement ear-tag identification during visual observation.

Activity data were collected using an automated data-collection system consisting of four 4-element, yagi antennas mounted on a 3.7-m pole and oriented at right angles to each other. The antennas were connected to a small computer (DCC 5040) and receiver. The computer controlled the receiver's scanning of radiocollar frequencies and recorded collar pulses from a deer for 1 min. The number of 1-min intervals recorded per hour for a given deer depended on whether the deer was within detection range and how many other deer also were detected and monitored. For each minute's collection of pulse rates, the mean pulse rate was calculated and then made relative to the radiocollar's base rate. Thus, a collar with no movement (50–60 pulses/min) produced a relative mean pulse rate of 100%. The system was rotated among three elevated locations every 3–4 days to cover about one-half the study area. Specific activities (bedding, standing, feeding, walking, and running) could not be accurately identified in this study or in any other because of the similarity of head and neck movement among different activities (e.g., bedding versus standing). However, active (feeding, walking, and running) deer could be discriminated from inactive (bedding and standing) deer 81% of the time (Relyea et al., in press).

Monitoring of activity took place during 16 November 1990–15 February 1991. Activity data were analyzed for gender, breeding period, and bihourly effects using analysis of variance. Breeding periods were defined as prerut (16 November–15 December), peak rut (when the majority of successful copulations occur; 16 December–15 January), and postrut (16 January–15 February) based on Kucera (1978) and M. T. Pittman (in litt.). For each deer, the 1-min mean pulse rates were averaged within a 2-h interval. This removed differences in sample sizes per interval. Any deer missing data from more than four 2-h intervals within a breeding period was not used. Missing data for a interval were filled using a weighted-value method for a split-plot design (Steel and Torrie, 1980).

The experimental design was repeated measures with gender as fixed, between-treatment effect and period and hour as the random, within-treatment effects. Assumptions of normality, homoscedasticity, and sphericity were tested where appropriate. Two-way analysis of variance for breeding periods and hours was computed within each gender to help elucidate the cause of the interaction of gender by breeding period by hour that occurred. Similarly, a two-way analysis of variance was computed for genders and periods using mean activity across all hours within a period. One-way analysis of variance was used to test for hourly differences within each period and gender. All treatments were considered significantly different at $P < 0.05$. Because the study was spatially replicated in other areas of southwestern Texas, care must be exercised when extrapolating these results to other populations of mule deer.

We used relocation estimates and visual observations to help explain differences in activity among breeding periods. Relocation estimates were used to examine movements of mule deer outside of their established home range. Dasmann and Taber (1956) and Zwickel et al. (1953) noted that male Columbian black-tailed deer (*O. h. columbianus*) traveled outside of their home range during the rut "apparently in search of receptive does" (Dasmann and Taber, 1956:155). Female black-tailed deer sometimes left their home range, but they did not travel as far. Following the breeding season, deer returned to their previously established home range. Whether this increased traveling was more predominant during prerut, peak rut, or postrut is not clear from the description.

Our relocations of collared deer let us estimate a home range for each animal and the amount of traveling that occurred outside of the home range during each breeding period. Deer were relocated using a different telemetry system from the one used for activity monitoring. It was a null-peak system of three receiving antennas (mobile and permanent), each with a standard error of 2.58°. Relocation accuracy was estimated following the guidelines of White and Garrott (1990). We used the relocations from 1 June to 15 November 1990 to define a deer's established home range using the minimum-convex-polygon estimator (Dalke and Sime, 1938). The percentage of relocations found inside and outside of the established home range from 16 February to 31 May 1991 (when deer should have returned to their previously established home range) was used as an index to the probability that a relocation might be found outside the estimated home range without the animal actually leaving. As White and Garrott (1990) noted, there will always be some points found outside of the home range because boundaries are based only on where we have previously relocated the animal and ot necessarily on everywhere the animal has ever been. This index allowed us to compare normal movement of deer outside of a home range (16 February to 31 May) to the percentage of points that were outside of the home range during each breeding period. Because of the small number of relocations within each breeding period (four, one, and six per deer during prerut, peak rut, and postrut, respectively), data for all deer were pooled.

Visual observations were made during the 2–3 h after dawn and before dusk using focal sampling (Altmann, 1974) of marked and unmarked deer. Breeding behaviors, including sparring, tending, circling, antler thrashing, and fighting, were noted and used to verify dates for the peak-rut period (Geist, 1981; Kucera, 1978). An index of tending behavior was created by multiplying the number of males tending by the number of females being tended when males and females were observed together. Sparring, circling, and antler thrashing indices were calculated by dividing the number of events observed by the number of males observed. All indices were averaged for 0.5-month intervals from 1 November to 28 February. The extra 0.5 month before prerut and after postrut were included for comparison of behavior less affected by breeding.

Observations of breeding behavior included additional behaviors of deer. For each observation of deer, time walking, feeding, and doing "other" behaviors (such as grooming, excreting, and breeding-related behaviors) was noted. Our objective in using these three categories was to observe how the deer might vary the amount of time they devote to walking and feeding during the 3-month breeding season. Mean percentages were calculated separately for males and females for 6-month periods from 16 October 1990 to 15 April 1991. Extending observations beyond the limits of the breeding season permitted comparison of behavioral percentages during the three breeding periods with periods less influenced by breeding. The total viewing effort was 338 h.

Results

The final sample size for activity of deer was affected primarily by the system's ability to detect deer at long ranges. Of the 34 deer sampled at least once by the data-collection computer, only 16 (13 males and three females) offered enough data for complete analysis. The mean (± 1 *SE*) number of activity estimates per deer per breeding period was 254 (135) with 1.9% missing data and the mean (± 1 *SE*) number of activity estimates per deer per period per hour was 21 (12).

TABLE 1.—*Relative activity* ($\bar{X} \pm 1$ SE) *of mule deer by gender and period during 16 November 1990–15 February 1991 in southwestern Texas. Activity values are percentages relative to a motionless radiocollar. Means with the same letter are not significantly different* ($P > 0.05$).

		Period		
Gender	*n*	Prerut	Peak rut	Postrut
Male	13	186 ± 7 A	211 ± 6 B	224 ± 9 C
Female	3	158 ± 9 A	180 ± 11 B	231 ± 32 C

The overall analysis revealed that relative activity of deer differed among periods ($P < 0.0001$), but not between genders ($P < 0.234$). There was no two-way interaction between gender and period ($P < 0.111$), gender and hour ($P < 0.969$), or period and hour ($P < 0.145$), but there was a three-way interaction ($P < 0.002$, Table 1). The two-way analysis of only gender and period showed that relative activity was lower during prerut than either peak rut or postrut ($P < 0.028$ and $P \leq 0.001$, respectively), and peak rut activity was lower than postrut ($P < 0.004$).

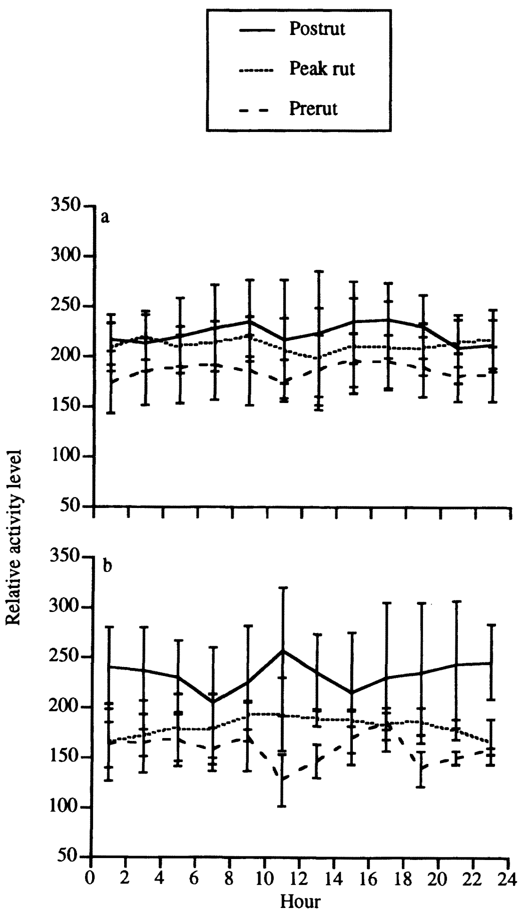

FIG. 1.—Mean (±1 *SE*) relative activity of male (a) and female (b) mule deer from 16 November 1990 to 15 February 1991 in southwestern Texas.

The two-way analyses of period and hour within each gender elucidated the cause of the three-way interaction. Within the males, there was no period-by-hour interaction ($P < 0.106$), but, within the females, there was ($P < 0.001$). Thus, the cause of the three-way interaction was the different diel patterns that females exhibited among the three-breeding periods (Fig. 1). Within some gender and breeding periods, the diel patterns had significant differences among hours of the day. Male deer tended to be crepuscular during prerut, more constant during peak rut, and crepuscular during postrut, but none of the breeding periods showed significant overall effects (prerut, $P < 0.106$; peak rut, $P < 0.586$; postrut, $P < 0.142$). Females were sharply crepuscular during prerut ($P < 0.002$) but had nearly equal activity during all 2-h intervals of peak rut ($P < 0.644$). During postrut, the activity pattern of females was the reverse of prerut with the lowest activity during early morning and evening and the greatest activity during midday, although the overall effect was not significant ($P < 0.089$).

The patterns observed in females were based on a small sample of three females that were successfully monitored for 3 months. Several deer were monitored for 1 or 2 of the 3 months and provided infor-

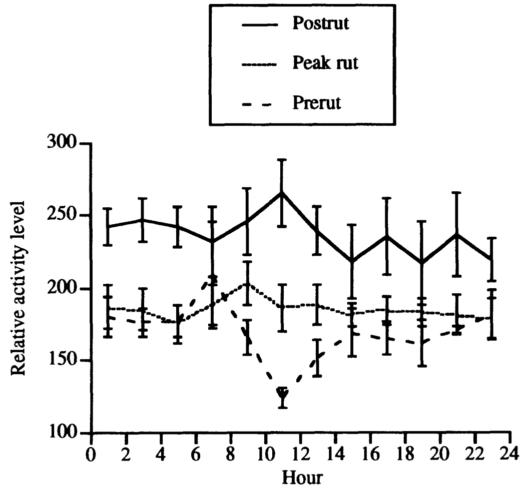

FIG. 2.—Mean (±1 *SE*) relative activity of eight female mule deer with incomplete data during prerut, nine during peak rut, and five during postrut, 16 November 1990–15 February 1991, in southwestern Texas.

mation as to the representatives of the three females. The trends shown by the eight, nine, and five females during prerut, peak rut, and postrut, respectively, were similar to those of the three females with complete data (Fig. 2).

Relocations of deer showed gender differences in movement trends (Table 2). A mean of 26 relocations/deer was used to define the home range during 1 June–15 November, and a mean of 15 relocations/deer during 16 February–31 May defined regular movement in and out of the home range; this movement was nearly equal for males and females. One of the 13 males shifted his home range in the spring, and he was excluded from this descriptive analysis. Males showed more concentrated movement during prerut and regular movement during peak rut; during postrut, movements were much more dispersed. The three females showed more concentrated movement during prerut, highly dispersed movement during peak rut, and concentrated movement during postrut. The large increase during peak rut was likely spurious given it was based upon only three relocations. Because there is the question of how representative these three females were of movement of females in general, we also compared the movements of an additional 16 females being relocated for other research, but not monitored for activity. These deer displayed regular movement during prerut and postrut and a moderate increase in traveling outside of the home range during peak rut.

Visual observations indicated seasonal trends in breeding-related behaviors of males (Fig. 3). Sparring, thrashing, and circling were most frequent during prerut; whereas, tending was most frequent during peak rut. The only highly aggressive behavior, or "serious" fight (Geist, 1981), was observed on 7 December. Copulations were never observed.

The percentages of walking, feeding, and other behaviors visually observed changed

TABLE 2.—*The percentage of relocations of mule deer found outside of an established home range (relocations from 1 June to 15 November 1990) during three breeding periods in southwestern Texas. Deer monitored for activity (*n *= 12 males, 3 females) were a subset of the larger group of deer (*n *= 12 males, 19 females) that were being relocated. Regular movement inside and outside of an estimated home range during 16 February to 31 May is provided for comparison. Numbers in parentheses are the number of pooled relocations found outside of a home range in relation to the total number of relocations.*

Time of year	Monitored males		Monitored females		All females	
16 November–15 December (prerut)	20	(8/40)	15	(2/13)	27	(34/91)
16 December–15 January (peak rut)	33	(3/9)	67	(2/3)	47	(11/21)
16 January–15 February (postrut)	54	(32/59)	28	(4.5/16)	36	(62/147)
16 February–31 May	31	(58/184)	18	(8/44)	33	(128/312)

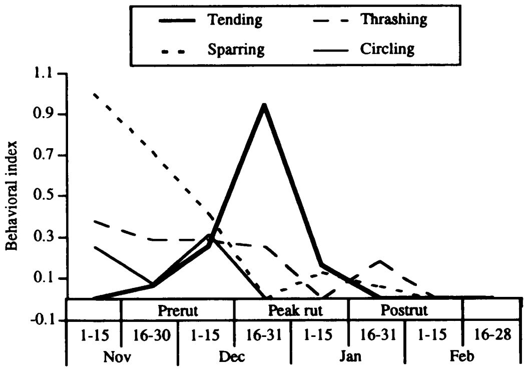

FIG. 3.—Behavioral indices for male mule deer from 1 November 1990 to 31 February 1991 in southwestern Texas.

greatly during the months of observation (Fig. 4). Male deer increased their daily proportion of walking and decreased their proportion of feeding throughout the breeding season. Following postrut, walking decreased and feeding increased. Behavior classified as "other" was the greatest during prerut and consisted primarily of agonistic male-male interactions. Behavioral trends of females were similar to the male trends, but the increase in feeding following postrut was much greater, with a concomitant decrease in walking.

DISCUSSION

The lack of difference in activity between male and female cervids during the breeding season also was reported by Beier and McCullough (1990), who found that rutting white-tailed deer in Michigan did not differ in percentage of active hours. However, they did note that males became more active than females at night and females were more active than males during the day. Clutton-Brock et al. (1982) also noted equivalent activity between genders in rutting red deer.

The crepuscular activity that we found during prerut and postrut in males and during prerut in females is common in cervids. Female elk in Colorado and both sexes of red deer in Germany had activity peaks at dawn and dusk throughout the year (Georgii, 1981; Georgii and Schroder, 1983; Green and Bear, 1990). White-tailed deer in Michigan were crepuscular, but those in Texas and Georgia also had a third peak around midnight during autumn (Beier and McCullough, 1990; Kammermeyer and Marchinton, 1977; Michael, 1970). Mule deer were crepuscular in Colorado (L. H. Carpenter, in litt.), Montana (Mackie, 1970), and Washington (Eberhardt et al., 1984). Thus, crepuscular activity patterns are common, but this study also suggested a previously undocumented change in activity for females during the breeding sea-

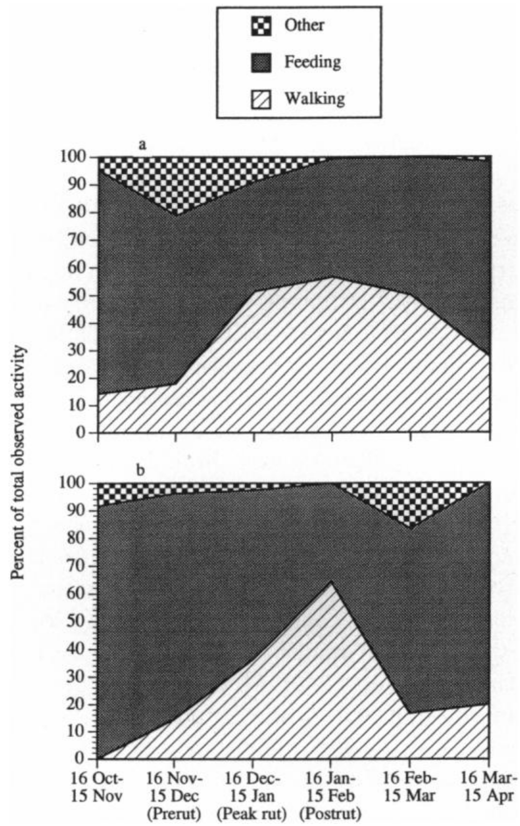

FIG. 4.—Percentages of behavior of male (a) and female (b) mule deer categorized as either walking, feeding, or "other" from 16 October 1990 to 15 April 1991 in southwestern Texas. Deer were visually observed within 3 h of sunrise and sunset.

son. Females shifted their diel pattern from crepuscular during prerut to constant during peak rut, followed by an inverse crepuscular pattern during postrut. Dasmann and Taber (1956:146) also observed that "deer become active throughout the day . . ." during peak rut. However, male and female Roosevelt elk *(C. e. roosevelti)* maintained their crepuscular pattern throughout their breeding season (Bowyer, 1981). A possible cause of changes of daily activity patterns of females could be harassment of females by males. Assuming our radiocollared females were bred during peak rut and a male could not differentiate a bred female from an unbred female until he approached her closely, pregnant females could reduce interactions with males by becoming less active during times of greatest activity of males and more active during times of lowest activity of males. This also may be the cause of Beier and McCullough's (1990) finding that male white-tailed deer are more active during the night while females are more active during the day. A corollary that can be tested in future research is that unbred females should maximize their interaction time with males and, thus, remain crepuscular during postrut.

The increased activity in males and females from prerut to peak rut was expected, but the additional increase from peak rut to postrut was not. No activity data on breeding mule deer could be found for comparison with our study. Ozoga and Verme (1975) witnessed a 28-fold increase in activity of penned female white-tailed deer during the 2- to 3-day period of proestrus and estrus. In Alabama (Ivey and Causey, 1981), female white-tailed deer had the most active daily patterns during the rut. In contrast, Holzenbien and Schwede (1989) found decreasing daytime activity from prerut to postrut among female white-tailed deer in Virginia; nighttime activity was unchanged. Thus, white-tailed deer apparently differ from mule deer in certain aspects of their breeding activity and behavior (see below). Pronghorns *(Antilocapra americana)* and red deer increased activity during the peak of the rut and then decreased it in the postrut (Georgii and Schroder, 1983; Kitchen, 1974). These latter observations probably were related to the territorial mating system of both species, which causes high energy expenditure during peak rut.

Increased activity of mule deer from prerut to peak rut to postrut could be due to day length, mate-searching, increased feeding, a shifted breeding season, or some combination of the four factors. First, increasing daylight could increase the activity level of deer. Georgii (1981) found a positive correlation between the two variables, but the confounding effects of warmer temperatures and increased forage made the conclusions unclear. If changes in the amount of daylight (Kingston, 1989) were reponsible for the observed activity levels, then activity during prerut ($\bar{X}$ = 617 min light/day) should lie between that observed during peak rut ($\bar{X}$ = 610 min light/day) and during postrut ($\bar{X}$ = 642 min light/day). The results did not follow this pattern; thus, this hypothesis was rejected.

Perhaps activity of deer was dependent on mate-searching. Matings probably occur first between nearest neighbors and then among more distant neighbors. During prerut, few of the nearby females are in estrus and the males are just beginning to tend them and exclude other males. As the number of estrous females reaches a maximum, male tending of females and male exclusion of other males should increase, with a concomitant increase in activity. Once nearby females are bred, the males must travel farther during postrut to find females that are unmated and this increased traveling should result in increased relative activity. Thus, the strategy for males is to concentrate travel inside the home range during prerut and increase travel outside of their home range during peak rut and postrut, in search of the few widely scattered, unbred females that remain (adults in their second estrous cycle and yearlings coming into estrus later than adults—Swank, 1958; Taber, 1953). Females may increase traveling during peak rut to increase the probability of being found by a male. Once bred, females resume their normal home range and alter their diel activity pattern to try to avoid harassment by males. Harassment by males undoubtedly still occurs, and avoidance of males may be partially responsible for the increase in activity of females during postrut. Further, if this scenario were true, both males and females should increase the percentage of time spent walking and running from prerut to postrut. Our data from activity, visual observation, and relocation support this hypothesis. However, given the paucity of relocations during peak rut (one fix per deer, pooled), we must be cautious in making firm conclusions about relocation data during this period.

White-tailed deer have a different chronology of breeding behaviors. Like mule deer, male white-tailed deer also move outside of their normal home range, but only during peak rut (Guyse, 1978; Hosey, 1980). In apparent contrast to female mule deer, Ivey and Causey (1981) found that female white-tailed deer move shorter linear distances per day and use a smaller percentage of their home range per day during peak rut than during prerut or postrut, and their movements during peak rut involve a greater amount of crisscrossing in a smaller area. The authors explained this pattern as a strategy to concentrate urine to attract males. Therefore, white-tailed deer are most active during peak rut because males are traveling outside of their home range searching for females and females are walking intensively in a small area to attract males. During postrut, both behaviors cease, and activity returns to prerut levels.

Another hypothesis for the increase in activity and traveling during postrut was a need for deer to increase forage intake to make up for energy reserves spent during peak rut. If foraging were responsible for the increase in activity from peak rut to postrut and we assume that forage became less available over time, deer should increase their time walking in search of forage from peak rut to postrut and even after postrut. The changes in walking, feeding, and other behavioral patterns that we observed visually indicated that the time males devoted to feeding remained about the same during peak rut and postrut while feeding time of females decreased. During this same period, the time spent walking increased in both genders. However, after postrut, the time that males and females spent feeding increased and the time spent walking decreased dramatically. This finding suggests that an increase in walking during the postrut was not necessary to find food, and we conclude that the increase in activity from peak rut to postrut was not due to increased feeding.

The final hypothesis was that the breeding periods were misclassified. If they were correctly classified, tending and antler thrashing should have been most frequent during peak rut, and sparring and circling should have been most frequent during prerut (Kucera, 1978). Tending, sparring, and circling followed the predictions, but antler thrashing did not. Tending is likely the most reliable index to breeding and, thus, we believe that the breeding periods were correctly classified. Additionally, Kucera's (1978) behavioral observations of mule deer in nearby Big Bend National Park, Pittman's (1987) back-dating of fetuses from mule deer in southwestern Texas, and Swank's (1958) work in Arizona all place peak rut around 1 January, suggesting that the timing of peak rut is quite constant from year to year.

Increased traveling, tending, and walking, and decreased feeding during peak rut, combined with reports of secondary copulation peaks during postrut, support the hypothesis that mate-searching was the most probable cause of increased activity in mule deer from prerut to postrut. These results have important implications for the applied ecologist whose goal is population regulation. An understanding of temporal changes in activity patterns of mule deer both within a day and among breeding periods, combined with information on the amount of traveling that occurs, could be used to increase or decrease interactions with humans and design harvest regimes to better regulate human-induced mortality in populations of deer. The high amount of traveling and the low amount of foraging by males, particularly during postrut, combined with less available forage, helps explain why mortality increases after the breeding season (S. Demarais et al., in litt.). Further studies should examine activity following the postrut and the amount of time it takes for the deer to return to the lower activity levels in prerut and more intensively investigate the proximate causes of circadian shifts in activity.

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Literature Cited

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour, 49:227–267.

Beier, P., and D. R. McCullough. 1990. Factors influencing white-tailed deer activity patterns and habitat use. Wildlife Monographs, 109:1–51.

Bowyer, R. T. 1981. Activity, movement, and distribution of Roosevelt elk during rut. Journal of Mammalogy, 62:574–582.

Clutton-Brock, T. H., F. E. Guiness, and S. D. Albon. 1982. Red deer: behavior and ecology of two sexes. The University of Chicago Press, Chicago, 378 pp.

Cohen, W. E., R. J. Reiner, F. C. Bryant, D. L. Drawe, and L. C. Bradley. 1989. Daytime activity of white-tailed deer in response to short-duration and continuous grazing. The Southwestern Naturalist, 34:428–431.

Correll, D. S., and M. C. Johnston. 1979. Manual of the vascular plants of Texas. University of Texas Press, Dallas, 881 pp.

Craighead, J. J., F. C. Craighead, Jr., R. L. Ruff, and B. W. O'Gara. 1973. Home ranges and activity patterns of nonmigratory elk of the Madison drainage herd as determined by biotelemetry. Wildlife Monographs, 33:1–50.

Dalke, P. D., and P. R. Sime. 1938. Home and seasonal ranges of the eastern cottontail in Connecticut. North American Wildlife Conference, 33:659–669.

Dasmann, R. F., and R. D. Taber. 1956. Behavior of Columbian black-tailed deer with reference to population ecology. Journal of Mammalogy, 37:143–164.

Eberhardt, L. E., E. E. Hanson, and L. L. Cadwell. 1984. Movement and activity patterns of mule deer in the sagebrush-steppe region. Journal of Mammalogy, 65:404–409.

Geist, V. 1981. Adaptive strategies in mule deer. Pp. 157–223, *in* Mule and black-tailed deer of North America (O. C. Wallmo, ed.). University of Nebraska Press, Lincoln, 605 pp.

Georgii, B. 1981. Activity patterns of female red deer (*Cervus elaphus*) in the Alps. Oecologia (Berlin), 49:127–136.

Georgii, B., and W. Schroder. 1983. Home range and activity patterns of male red deer (*Cervus elaphus L.*) in the Alps. Oecologia (Berlin), 58:238–248.

Green, R. A., and G. D. Bear. 1990. Seasonal cycles and daily activity patterns of Rocky Mountain elk. The Journal of Wildlife Management, 54:272–279.

Guyse, K. D. 1978. Activity and behavior of unhunted white-tailed deer bucks during the rut in Southwest Alabama. M.S. thesis, Auburn University, Alabama, 141 pp.

Holzenbien, S., and G. Schwede. 1989. Activity and movements of female white-tailed deer during the rut. The Journal of Wildlife Management, 53:219–223.

Hosey, A. G., Jr. 1980. Activity patterns and notes on behavior of male white-tailed deer during rut. M.S. thesis, Auburn University, Alabama, 66 pp.

Ivey, T. L., and M. K. Causey. 1981. Movements and activity patterns of female white-tailed deer during rut. Proceedings of the Southeastern Association of Fish and Wildlife Agencies, 35:149–166.

Kammermeyer, K. E., and R. L. Marchinton. 1977. Seasonal change in circadian activity of radio-monitored deer. The Journal of Wildlife Management, 41:315–317.

Kingston, M. (ed.). 1989. Texas almanac. The Dallas Morning News, Dallas, Texas, 607 pp.

Kitchen, D. W. 1974. Social behavior and ecology of the pronghorn. Wildlife Monographs, 38:1–96.

Kucera, T. E. 1978. Social behavior and breeding system of the desert mule deer. Journal of Mammalogy, 59:463–476.

Kufeld, R. C., D. C. Bowden, and D. L. Schrupp.

1988. Habitat selection and activity patterns of female mule deer in the Front Range, Colorado. Journal of Range Management, 41:515–522.

MACKIE, R. J. 1970. Range ecology and relations of mule deer, elk and cattle in the Missouri River Breaks, Montana. Wildlife Monographs, 20:1–79.

MCCULLOUGH, D. R. 1982. Evaluation of night spotlighting as a deer study technique. The Journal of Wildlife Management, 46:963–973.

MICHAEL, E. D. 1970. Activity patterns of white-tailed deer in South Texas. The Texas Journal of Science, 21:417–438.

MILLER, F. L. 1970. Distribution patterns of black-tailed deer (*Odocoileus hemionus columbianus*) in relation to environment. Journal of Mammalogy, 51: 248–260.

NEWHOUSE, S. J. 1973. Effects of weather on behavior of white-tailed deer of the George Reserve, Michigan. M.S. thesis, The University of Michigan, Ann Arbor, 154 pp.

OCKENFELS, R. A., AND J. A. BISSONETTE. 1984. Temperature-related responses in north-central Oklahoma white-tailed deer. Pp. 64–67, *in* Deer in the Southwest: a symposium (P. R. Krausman and N. S. Smith, eds.). School of Natural Resources, University of Arizona, Tucson, 131 pp.

OZOGA, J. J., AND L. J. VERME. 1975. Activity patterns of white-tailed deer during estrus. The Journal of Wildlife Management, 39:679–683.

RELYEA, R. A., I. M. ORTEGA, AND S. DEMARAIS. In press. Activity monitoring in mule deer: assessing telemetry accuracy. Wildlife Society Bulletin.

RENECKER, L. A., AND R. J. HUDSON. 1989. Seasonal activity budgets of moose in aspen-dominated boreal forests. The Journal of Wildlife Management, 53: 296–302.

STEEL, R. D. G., AND J. H. TORRIE. 1980. Principles and procedures of statistics. McGraw-Hill Book Company, New York, 633 pp.

SWANK, W. G. 1958. The mule deer in Arizona chaparral. Arizona Game and Fish Department, Phoenix, 109 pp.

TABER, R. D. 1953. Studies of black-tailed deer reproduction on three chaparral cover types. California Fish and Game, 39:177–186.

UNITED STATES DEPARTMENT OF COMMERCE. 1990. Climatological data, Texas. National Oceanic and Atmospheric Administration, Ashville, North Carolina, 95:1–76.

———. 1991. Climatological data, Texas. National Oceanic and Atmospheric Administration, Ashville, North Carolina, 96:1–76.

WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, 383 pp.

ZWICKEL, F., G. JONES, AND H. BRENT. 1953. Movement of Columbian black-tailed deer in the Willapa Hills area, Washington. The Murrelet, 34:41–46.

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