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Nocturnal activity of female desert mule deer

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The University of Arizona, 1992

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NOCTURNAL ACTIVITY OF FEMALE DESERT MULE DEER

by

Charles Laforest Hayes

**A Thesis Submitted to the Faculty of the
WILDLIFE AND FISHERIES SCIENCE
In Partial Fulfillment of the Requirements
For the Degree of
MASTER OF SCIENCE
In the Graduate College
THE UNIVERSITY OF ARIZONA**

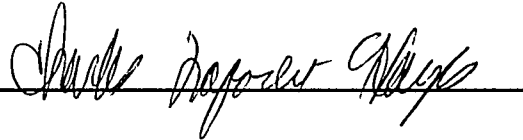
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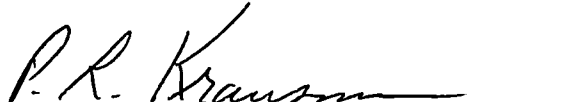
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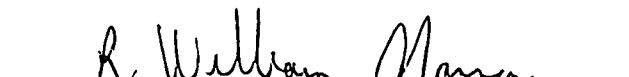



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ABSTRACT

I quantified nocturnal activity of female desert mule deer (Odocoileus hemionus crooki) in the Belmont and Bighorn mountains, Arizona, 1990. I monitored 5 radio-collared deer and estimated activity with a digital processor. I determined seasonal differences in percent of time active and distances moved at night from locations of radio-collared deer. I compared nocturnal home ranges and habitat use to those obtained from daytime locations. Activity differed between seasons ($P = 0.046$). Nocturnal activity was greatest in spring and summer, and decreased in winter. Movement distances also varied with seasons ($P = 0.045$). Most nocturnal locations (88%) occurred within daytime home ranges. Use of habitat in relation to availability was consistent between day and night for 6 of 8 vegetation associations. Use of disturbed sites increased at night ($P < 0.01$).

INTRODUCTION

Mule deer and black-tailed deer (Odocoileus hemionus) in North America occupy climatic zones ranging from taiga to semiarid tropics (Wallmo 1978). Desert mule deer inhabit the southern portion of this range and are therefore subjected to heat and drought more than the northern subspecies. Behavioral and/or physiological adaptations to desert environments are necessary for survival. In African deserts, the eland (Taurotragus spp.) and oryx (Oryx spp.) can survive indefinitely without drinking due to adaptations such as tolerance of body temperature fluctuations and efficient oxygen uptake to reduce respiratory water loss (Taylor 1969). In contrast, mule deer exhibit no specialized physiological mechanisms for water conservation (Knox et al. 1969). Hervert and Krausman (1986) concluded that desert mule are at least behaviorally dependent upon available drinking water. One behavioral adaptation of desert animals is to be active during nocturnal hours when temperatures are less extreme; however, relatively little is known about the nocturnal activity of desert mule deer.

Nocturnal behavior is an important component of the daily activity cycle for mule deer and white-tailed deer (Odocoileus virginianus), especially during warmer

seasons. White-tailed deer in Georgia had daytime:nighttime activity ratios of 1:2.2 and 1:2.0 for males and females, respectively, during summer and fall (Kammermeyer and Marchinton 1977). The majority of summer movements of white-tailed deer in Oklahoma occurred at night (Ockenfels and Bissonette 1984). Columbian black-tailed (O. h. columbianus) deer in northern California also were reported to feed throughout the night during summer (Taber and Dasmann 1958). Desert mule deer in southeast Arizona were rarely seen active during the hot and dry season, and were assumed to be predominantly nocturnal during this time (Anthony and Smith 1977).

A general pattern of nocturnal activity of white-tailed deer was described by Montgomery (1963). Deer generally grazed in fields until midnight, then bedded in woods, and became active in upper woodlands again 1-2 hours before sunrise. Other studies have shown the importance of early-night hours in the daily activity cycle of deer. White-tailed deer in Georgia had activity peaks between 1800-2200 hours in summer and fall (Kammermeyer and Marchinton 1977). Activity of Columbian black-tailed deer in northwestern Oregon was characterized by strong crepuscular peaks from June to August, with a weaker twilight peak in September (Miller

1970). In south-central Washington, Eberhardt et al. (1984) identified a peak in mule deer activity from 1800-2100 hours. Crepuscular periods were reported to be the principal times for desert mule deer to move to drinking water (Elder 1954). These data suggest that descriptions of deer behavior, home ranges, or habitat use patterns based only on daytime observations may be incomplete.

Hypotheses regarding influences on activity of deer often are based upon seasonal patterns of habitat use and concurrent changes in amount and timing of activity. Montgomery (1963) concluded that the pattern of grazing in fields during nocturnal hours while spending most of the daytime hours in wooded areas reflected attempts to avoid human disturbances. Seasonal changes in the amount of time spent bedded versus foraging were believed to result from changes in the length of time required to find sufficient forage (Montgomery 1963). A similar pattern of use of fields at night and woodlands during daylight by white-tailed deer was observed in Michigan, but only during spring (McCullough 1982). Maximum levels of nocturnal activity occurred in April-May, close to the time of spring green-up and high forage availability in fields (McCullough 1982). Ockenfels and Bissonette (1982) found white-tailed deer in Oklahoma to reduce activity in July-August to 42% of activity levels

observed in December-January. Use of all vegetation associations except riparian areas decreased as ambient temperatures reached >30 C, possibly resulting from selection of a cooler microclimate and/or protective escape cover for bedded deer (Ockenfels and Bissonette 1984). Rautenstrauch and Krausman (1989) concluded that desert mule deer in southwestern Arizona migrated an average of 14.2 km to areas containing available drinking water during the summer dry season.

Mule deer inhabiting desert environments would be expected to exhibit behavioral adaptations to heat and limited water. Potential adaptations include large home ranges, movements toward areas of available water during dry periods, use of habitat (or microhabitat) for thermoregulation, and reductions in activity at high ambient temperatures. According to the hypotheses formulated by McNab (1963) and Harestad and Bunnell (1979), desert mule deer would be expected to have larger home ranges than mule deer living in more mesic environments. Desert mule deer in southwestern Arizona have home ranges of up to 145.2 km^2 , the largest home-range size ever reported for mule deer (Rautenstrauch 1987). Previous research on desert mule deer in the Belmont and Bighorn mountains of western Arizona indicated that home ranges are large ($\bar{x} = 89.5 \text{ km}^2$) but

that deer do not migrate to water sources (Krausman 1985). Deer in this area may not have to migrate outside their home ranges to find water because of the relatively high density of permanent, man-made water sources. When water catchments were "closed" Hervert and Krausman (1976) documented movement to water sources outside of diurnal home ranges. Reductions in activity of desert mule deer in high ambient temperatures were observed by Truett (1972), who reported daytime movements to consist only of moving between bedsites during summer. Increased nocturnal movements for drinking, feeding and other activities would be anticipated under these conditions, but have not previously been documented.

Despite its potential importance for management, relatively little is known of the nocturnal component of mule deer behavior. A previous study conducted in the Belmont and Bighorn mountains provided baseline data for the analysis of the effects of the Central Arizona Project (CAP) on desert mule deer (Krausman 1985). The CAP is a large canal which runs through desert mule deer habitat south of the Belmont and Bighorn mountains. Before the CAP was constructed, home ranges and use of vegetation associations were ascertained from daytime locations of radio-collared deer (Krausman 1985). Whether the addition of nighttime locations would

significantly change observed home ranges and/or habitat use patterns here or in other deer habitats is unknown. Although some parameters of mule deer ecology are not affected by time of day, examinations of use of water sources or topography should include nocturnal observations (Miller et al. 1984). My objectives were to quantify the extent of nocturnal activity and movement by desert mule deer over 1 year, and to compare the distribution of locations and patterns of habitat use to those found during the daytime.

STUDY AREA

The study was conducted in the Belmont and Bighorn mountains, located in western Maricopa County, Arizona. Elevations within the study area range from 415 m in the desert plains bordering the CAP to 1,060 m at Bighorn Peak.

The study area lies within the Mojave Sonoran Desert habitat province (Wallmo 1981). Nine vegetation associations were identified by Krausman (1985): triangleleaf bursage (Ambrosia deltoidea)-brittlebush (Encelia farinosa) northeast, triangleleaf bursage-brittlebush southwest, triangleleaf bursage-brittlebush volcanic, triangleleaf bursage-brittlebush foothills, triangleleaf bursage-transition, triangleleaf bursage-palo verde (Cercidium spp.) northeast, triangleleaf bursage-palo verde southwest, creosote (Larrea tridentata) flats, and disturbed sites resulting from construction of the CAP. I considered both aspects (northeast and southwest) of triangleleaf bursage-brittlebush to be a single vegetation association.

Seasons were defined as winter (Jan-Mar), spring (Apr-Jun), summer (Jul-Sep) and fall (Oct-Dec). These seasons were based upon climatological data from the Aguila weather station, located 40 km north of the study area (Krausman 1985). Mean annual precipitation in the

Belmont and Bighorn mountains is approximately 20 cm, and temperatures often exceed 45 C in the summer (Krausman 1985).

METHODS

Activity

Four radio-collared female deer were monitored during each season. One deer was replaced when it moved to an area where I was unable to obtain a clear signal from the radio collar. It was replaced with another female in the same area with a stronger radio transmitter. Only females were studied to eliminate differences due to sex. Studying females exclusively eliminated potential sex-specific variations in behavior occurring during the rut and hunting season. Female mule deer have smaller home ranges than males (Robinette 1966, Krausman 1985), and therefore were easier for me to locate at night. Roads leading into the Belmont and Bighorn mountains were generally 1.0-2.5 km apart. The low road density encouraged the use of female deer in the study to minimize the time spent locating each animal at night. During the daytime, each female deer was located visually approximately once every 4-5 days. Locations were obtained using a Telonics Model TR-2 Receiver (Telonics, Inc., Mesa, Ariz.), and a hand-held yagi antenna. Coordinates of each location were plotted using a Universal Transverse Mercator (UTM) grid. At each location I recorded vegetative association, behavior of deer, temperature, and humidity. Home ranges were

constructed using the minimum convex polygon method (Southwood 1966).

At night, deer were located by triangulation, using the same equipment as for daytime locations. Compass bearings were taken from 3 to 7 known points (e.g, mines, wells, road intersections, washes) within an average time span of 18 minutes. Triangulated locations were recorded only when ≥ 3 compass bearings came within 200 m of intersecting at a single point. When compass bearings did not intersect at one point, the location was placed in the center of the polygon.

Behavior was classified as inactive or active using a Telonics Model TDP-1 Digital Processor. Deer were considered inactive if the signal amplitude was maintained at an equilibrium level with < 2 changes/minute. This definition of inactivity has been previously used with tip-switch radio collars by Garshelis et al. (1982). It allowed for changes in signal amplitude due to head movements of bedded or standing deer without causing their behavior to be interpreted as active. Other telemetry studies of ungulate activity were able to identify behaviors correctly as active or inactive 95% of the time with moose (Alces alces) (Van Ballenberghe and Miquelle 1990) and 90% of the time with white-tailed deer

(Holzenbein and Schwede 1988). Using the same system as this study, Alderman et al. (1989) found activity data to agree with direct visual observation >93% of the time in a study of mountain sheep (Ovis canadensis mexicana).

Each week, data were collected on all 4 deer from 1 of 3 nocturnal periods: sunset-2200 hours, 2200-0200 hours and 0200-sunrise. Time segments were rotated in a random order so they were all equally represented within each season. Continuous activity data were collected from a single deer for the duration of the observation period. Deer that moved out of signal range were relocated as soon as possible. In the 2 instances when deer moved to an area where a strong signal could not be obtained, all activity data from the observation period were excluded from the analysis.

During the nocturnal observation periods, I recorded temperature and humidity hourly. I expressed activity as percent of minutes active for each hour of the night. Pearson product-moment correlations were calculated to quantify relationships between activity and temperature intervals (3 C in width) containing >10 observations each. I also examined correlations between activity and relative humidity intervals (10-30 observations each).

I analyzed differences in activity between seasons and months using analysis of variance (ANOVA) and Duncan

multiple range tests. Simultaneous contrasts of each season compared to all others were performed using Bonferroni t -tests. I used the arcsine-square root transformation on all percent activity data in an attempt to meet the assumptions of normality and homogeneity of variances.

I examined the effect of changes in moonlight on nocturnal activity. I identified 3 distinct periods of moonlight: full moon (± 3 days), new moon (± 3 days), and quarter moon (all other phases). I used ANOVA to test for differences in activity during these 3 periods.

I used contingency table analysis to examine seasonal differences in the behavior (active or inactive) of deer found during daytime. I constructed daytime temperature intervals of 7 C and calculated percent of daytime locations with deer found active for each interval. I used the same analysis for these temperature intervals as for nocturnal activity data. The wider daytime temperature intervals represent the smaller number of daytime locations and the binomial nature of the daytime activity data. Correlations between percent of locations active and relative humidity were examined using humidity intervals containing ≥ 10 observations each.

Movement and Habitat Use

Deer were located by triangulation at the beginning

and end of each observation period. Habitat type of each location and linear distance moved were recorded for each observation period. Chi-square analysis was used to determine differences in categories of movement distances between seasons and nocturnal observation periods. Locations of deer at night were used to construct minimum convex polygon (MCP) home ranges (Southwood 1966). These nocturnal home ranges were compared to home ranges constructed from daytime locations.

I obtained diurnal home ranges and habitat use patterns from visual locations of radio-collared deer. Twenty-four hour movement distances were calculated from the distance between relocations of deer on successive days. Differences between habitat use and availability during both day and night were tested using the G test for goodness of fit (Zar 1974). I examined differences between daytime and nighttime use of individual vegetative associations using 2 x 2 contingency tables.

Verification

I tested the accuracy of the methods used to measure nocturnal activity and to locate deer at night. Accuracy of the activity monitoring system was determined through the simultaneous observation of deer by 2 different methods. One observer classified the deer as active or inactive based upon visual observations, while the second

used the digital processor to classify behavior. The accuracy of triangulated locations was tested with the use of an unattached radio collar (White and Garrott 1990). One observer located a deer, and placed the radio collar at that locations. The second observer triangulated the location of the collar, and compared the distance between actual and triangulated locations.

RESULTS

Activity

I collected data for 590 hours during nocturnal periods. Classification of behavior as active or inactive made using the digital processor was accurate for 94% of the time over 5.3 hours I tested the system. This is similar to results obtained by Alderman et al. (1989) using the same system with mountain sheep.

Patterns of nocturnal activity varied within the year (Fig. 1). The only pattern of within-night activity that was observed throughout the year was an increase in activity during the hour previous to sunrise. In winter, summer, and fall, the highest level of nocturnal activity occurred during the first hour after sunset. Periods of lesser activity or "lulls" occurred within the night at different hours during different seasons. In winter, percent activity remained low (18.7-21.9%) from 2300-0100. In spring, the hours of least activity were 0200-0400 (46.7-48.0%). Activity in summer was also low from 0200-0300 (35.4-37.2%). In fall, the period of reduced activity was 1900-2100 (35.4-37.2%). Percent of time active differed significantly among the 3 nocturnal periods only during winter ($P = 0.012$).

Nocturnal activity of female desert mule deer differed among seasons ($P = 0.046$) and months

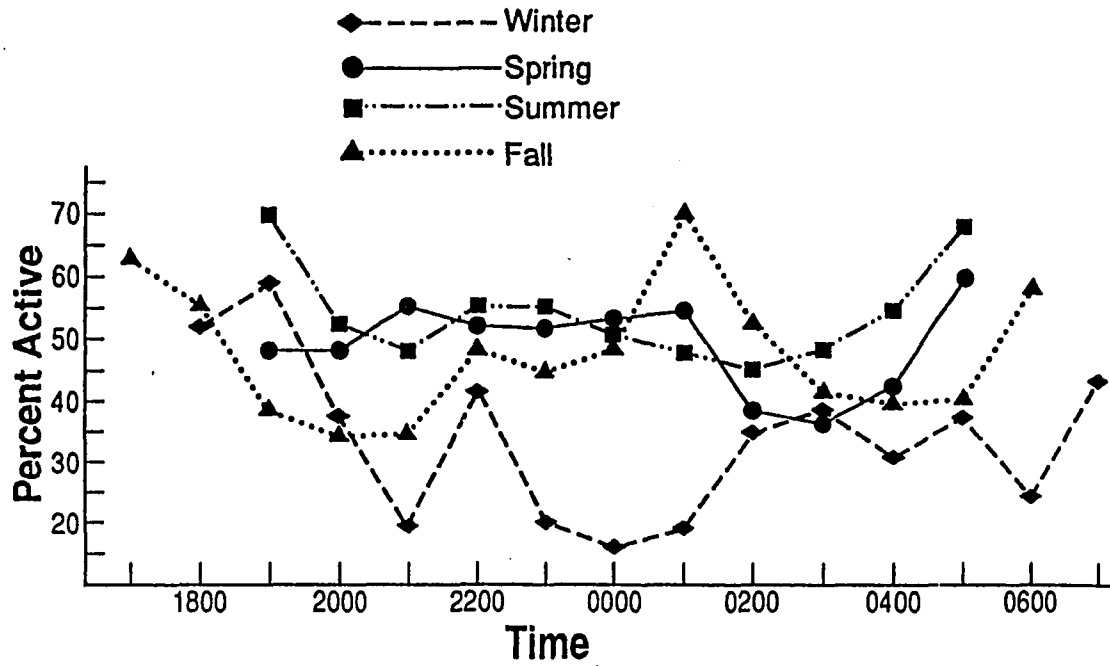


Fig. 1. Nocturnal activity of desert mule deer during 4 seasons in western Arizona, 1990. Percent activity data from all deer have been lumped together within each season.

($P = 0.029$). Multiple comparisons of seasonal activity showed significant differences between winter and spring and between winter and summer ($P < 0.05$). Contrasts between seasons showed significantly less nocturnal activity in winter compared to other all other seasons ($P < 0.05$). Nocturnal activity was greatest in August and lowest in February (Table 1).

Positive correlations between observed temperature and nocturnal activity were significant ($r = 0.92$, $P = .000$). Analysis of orthogonal polynomials revealed that only the linear component of the relationship between activity and temperature (both daytime and nighttime) was significant. However, this relationship was confounded with seasonal changes in activity. No correlations of mean activity and temperature within seasons were significant except during winter (Table 2). There was a negative relationship between mean activity and relative humidity during all 4 seasons. The only significant correlation occurred during spring. There was no significant difference in activity among the 3 periods of moonlight identified.

Percentages of active daytime locations for the 5 deer used in the analysis were 31.8, 23.7, 43.0, and 45.1% for winter, spring, summer, and fall, respectively. Frequency of active daytime locations was not independent

Table 1. Monthly nocturnal activity of female desert mule deer in the Belmont and Bighorn mountains, Arizona, 1990.^a

<u>Month</u>	<u>Activity</u>	<u>No. hours</u>
Jan	0.633ABC ^b	56
Feb	0.573A	52
Mar	0.584AB	47
Apr	0.745ABCD	52
May	0.782CD	61
Jun ^c	0.824	19
Jul	0.808CD	65
Aug	0.873D	58
Sep	0.805CD	26
Oct	0.763BCD	75
Nov	0.788CD	72
Dec ^c	0.459	9

^aPercent activity data are transformed using the arcsine-square root transformation.

^bActivity levels with the same letter are not different ($P > .05$).

^cJune and December were excluded from multiple comparisons because 2 deer were observed ≤ 5 hours during those months.

Table 2. Pearson product-moment correlation coefficients (r) and P values for relationships between activity^a, temperature (T), and relative humidity (RH) for desert mule deer in the Belmont and Bighorn mountains, Arizona, 1990.

Season ^b	T		RH	
	r	P	r	P
Winter	0.75	0.02*	-0.74	0.15
Spring	0.57	0.32	-0.84	0.03*
Summer	0.31	0.61	-0.17	0.79
Fall	0.01	0.98	-0.20	0.66

^aData transformed using the arcsine-square root transformation.

^bWinter = Jan, Feb, Mar; Spring = Apr, May, Jun; Summer = Jul, Aug, Sep; Fall = Oct, Nov, Dec.

of season ($P = 0.009$). There was a negative relationship between percent of active daytime locations and temperature intervals during all 4 seasons, but the only significant correlation occurred during spring ($r = -0.998$, $P = 0.003$). Deer were found active in only 1 of 27 daytime locations when ambient temperatures exceeded 37 C. There were no daytime observations of active deer above 39 C ($n = 13$). There was a positive relationship between activity of daytime locations and relative humidity during all seasons. Within seasons, the only significant correlation occurred during summer ($r = 0.84$, $P = 0.029$). Relative humidity recorded during nocturnal observation periods was high in winter and summer ($\bar{x} = 46.1$ and 43.7 %, respectively), and lowest in spring ($\bar{x} = 34.6$ %).

Movement

Desert mule deer moved an average distance of 2,275 m between visual relocations at 24-hour intervals. Average movement distance for nocturnal observation sessions was 778 m. The mean error distance for triangulated locations was 183m, with a 95% confidence limit of 237 m. To account for locational error, 84 nocturnal movements were placed in intervals of 0-499 m, 500-999 m, and $\geq 1,000$ m. Frequencies of interval distances by season were significantly different

($P = 0.04$). Mean distances moved were greatest during spring ($\bar{x} = 963$ m) and summer ($\bar{x} = 999$ m) (Table 3). Distances moved were smallest during the second (2200-0159) nocturnal observation period ($\bar{x} = 691$ m) (Table 4). Differences between observation periods were not significant.

Home Range and Habitat Use

Daytime MCP estimates of home ranges had a mean area of 32.3 km^2 and contained 1.6 permanent water sources ($n = 5$). Home range sizes during the nocturnal periods of each deer were based upon fewer independent locations and therefore smaller. Area observation curves indicated that approximately 60 locations were required to adequately sample the entire home range of animal, based on the criteria used by Odum and Kuenzler (1955). Three of 5 diurnal home ranges met these criteria, but nocturnal home ranges were constructed from an average of only 40 locations. Although no point locations of deer were recorded during the middle of an observation period, deer were followed closely enough to maintain a strong radio signal. Substantial nocturnal movements outside of daytime home ranges could have been detected, but were not observed during 198 nocturnal observation periods. Eighty-eight percent of nocturnal home ranges fell within daytime home ranges (Figs. 2-6). Nocturnal home ranges

Table 3. Distances moved (m) for female desert mule deer in Belmont and Bighorn mountains, Arizona, 1990.

Season ^a	\bar{x}	SE	n
Winter	496	83	20
Spring	963	124	23
Summer	999	116	20
Fall	636	110	21

^aWinter = Jan, Feb, Mar; Spring = Apr, May, Jun;
 Summer = Jul, Aug, Sep; Fall = Oct, Nov, Dec.

Table 4. Distances moved (m) during 3 nocturnal periods for female desert mule deer in the Belmont and Bighorn mountains, Arizona, 1990.

Time (hours)	\bar{X}	SE	n
Sunset-2159	816	104	29
2200-0159	691	93	30
0200-sunrise	837	114	25

- ◆..... Diurnal Home Range
- Nocturnal Home Range
- Permanent Water Source
- ▲ Mountain Peak

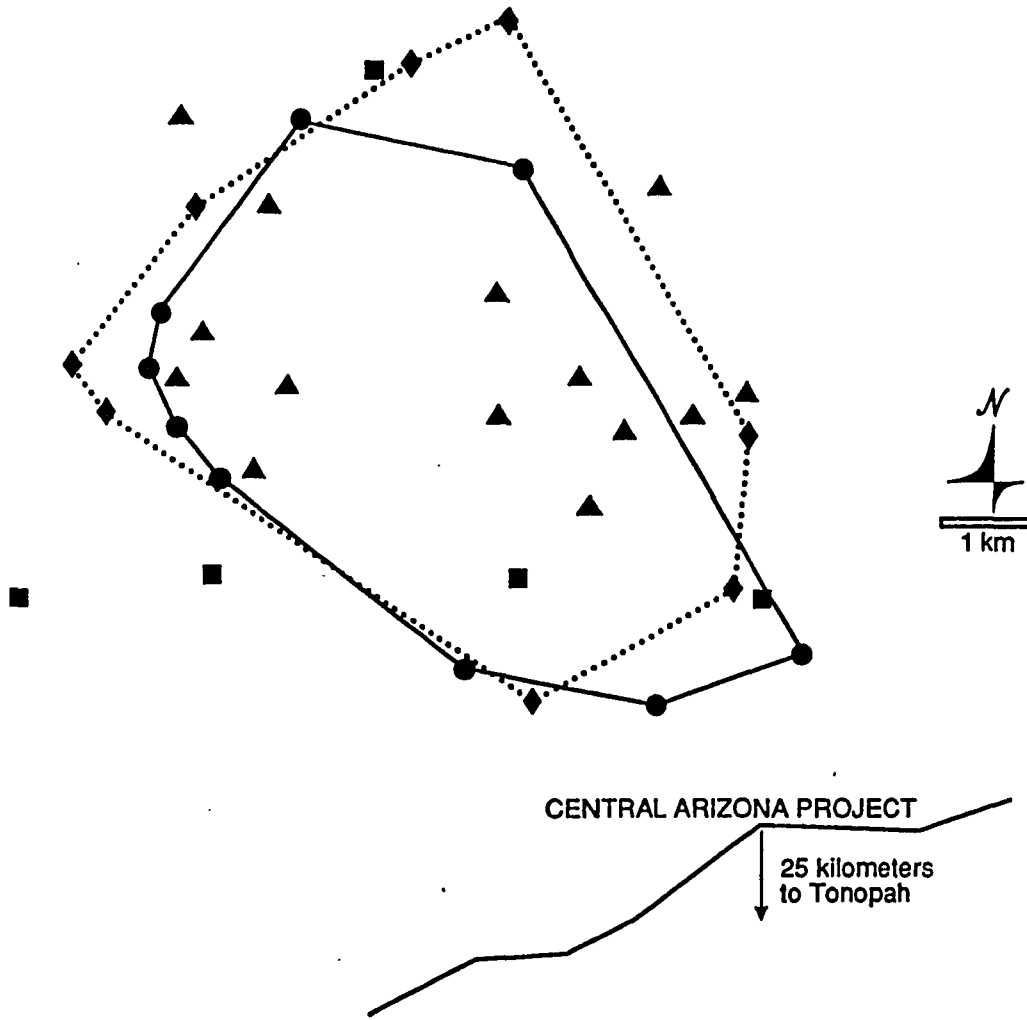


Fig. 2. Diurnal and nocturnal home ranges of deer 4020 in western Arizona, 1990. The areas of the MCP estimates for diurnal and nocturnal home ranges are 40.1 km² ($\underline{n} = 80$) and 33.3 km² ($\underline{n} = 44$), respectively.

- ◆..... Diurnal Home Range
- Nocturnal Home Range
- Permanent Water Source
- ▲ Mountain Peak

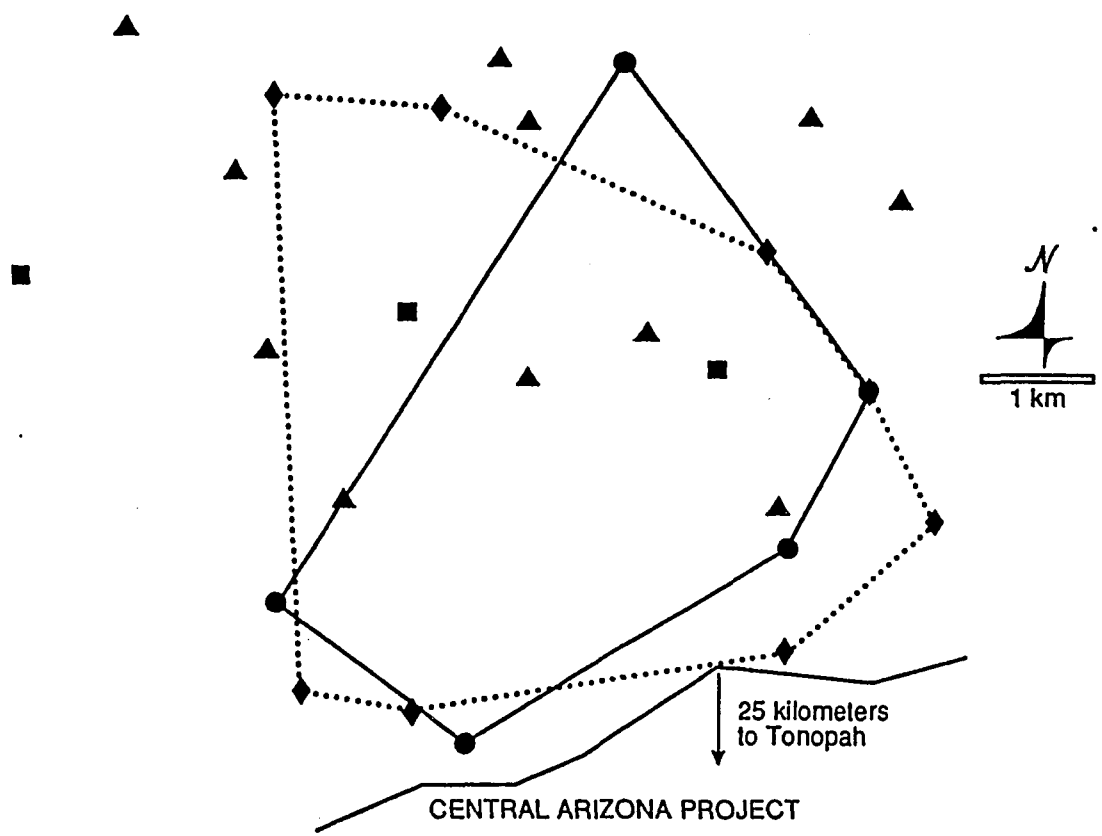


Fig. 3. Diurnal and nocturnal home ranges of deer 4120 in western Arizona, 1990. The areas of the MCP estimates for diurnal and nocturnal home ranges are 26.5 km² ($\bar{n} = 80$) and 18.4 km² ($\bar{n} = 51$), respectively.

- ◆..... Diurnal Home Range
- Nocturnal Home Range
- Permanent Water Source
- ▲ Mountain Peak

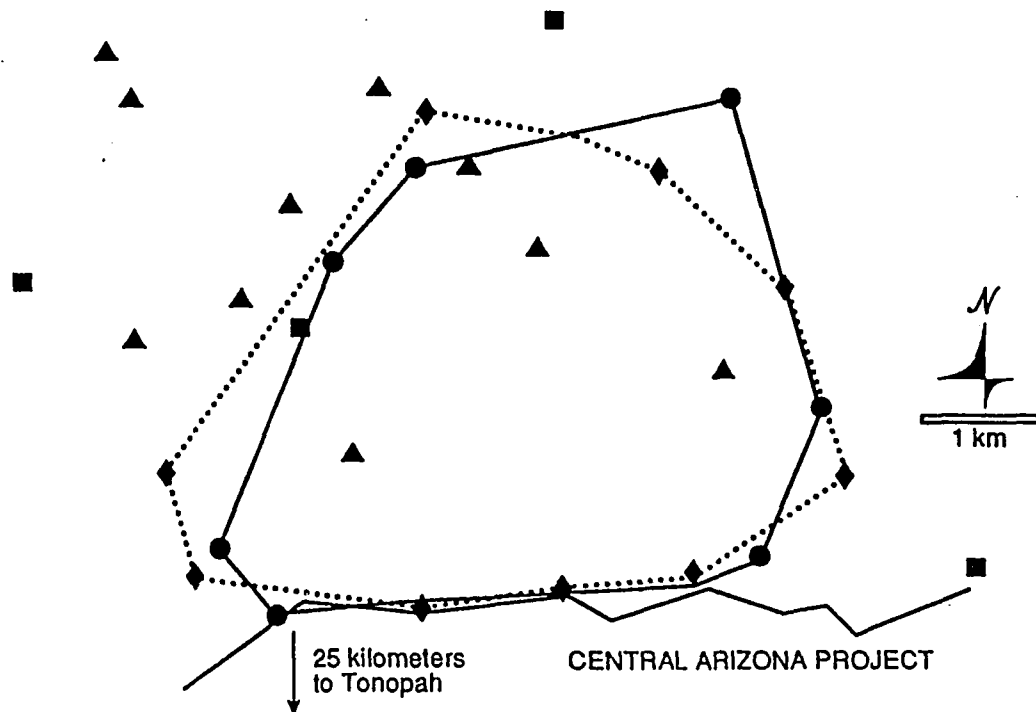


Fig. 4. Diurnal and nocturnal home ranges of deer 4570 in western Arizona, 1990. The areas of the MCP estimates for diurnal and nocturnal home ranges are 25.7 km^2 ($\underline{n} = 81$) and 24.7 km^2 ($\underline{n} = 51$), respectively.

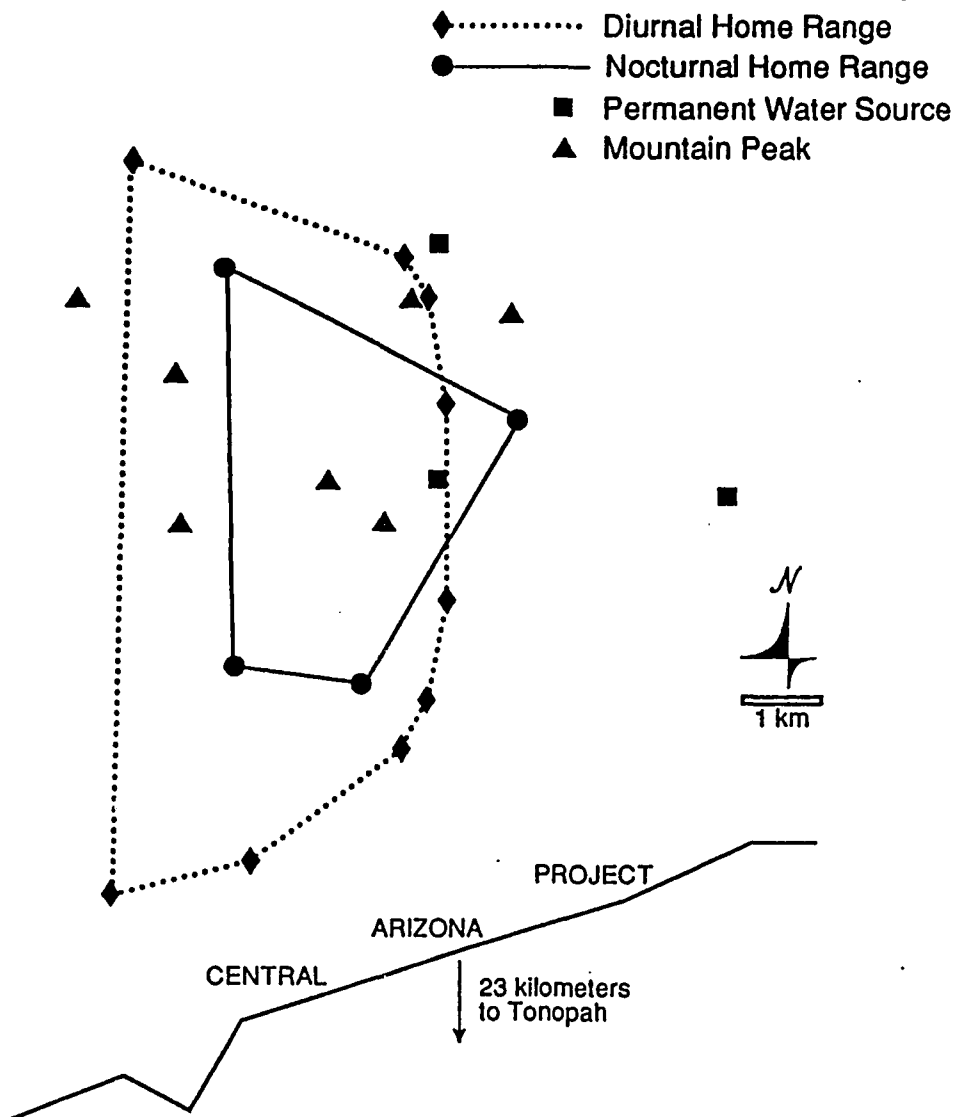


Fig. 5. Diurnal and nocturnal home ranges of deer 4850 in western Arizona, 1990. The areas of the MCP estimates for diurnal and nocturnal home ranges are 32.7 km^2 ($\underline{n} = 36$) and 23.2 km^2 ($\underline{n} = 24$), respectively.

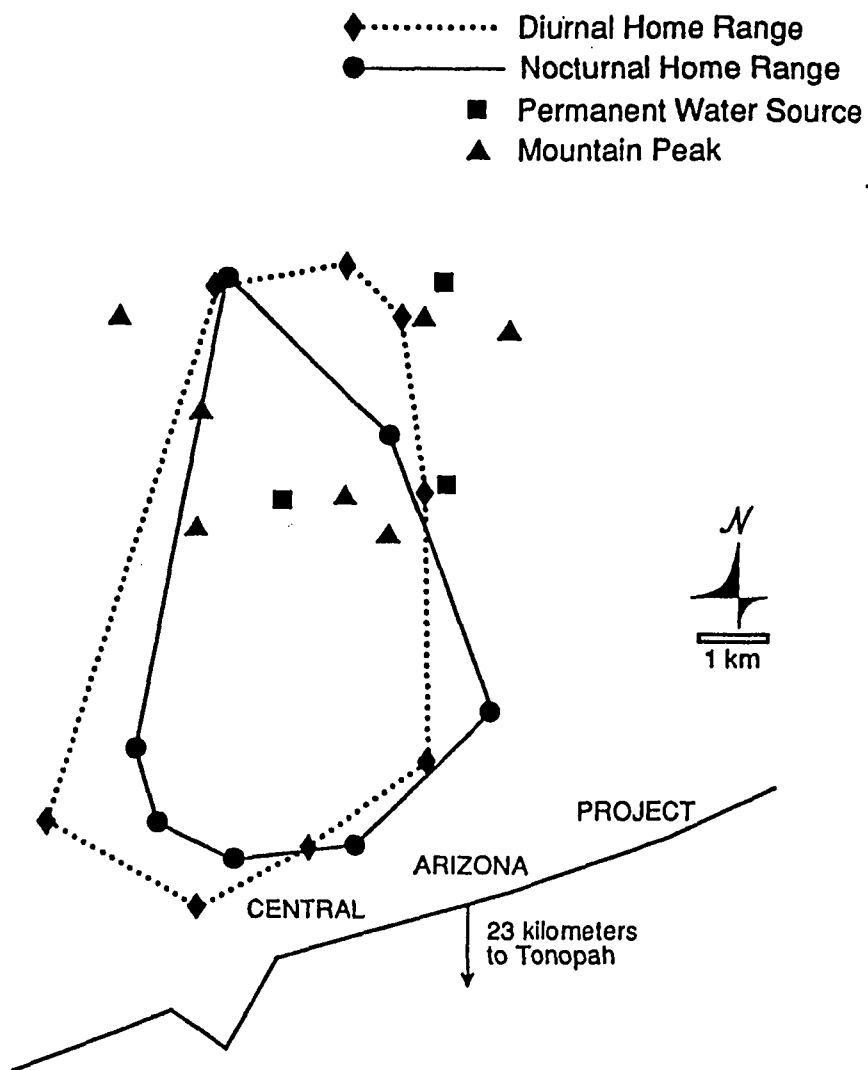


Fig. 6. Diurnal and nocturnal home ranges of deer 5260 in western Arizona, 1990. The areas of the MCP estimates for diurnal and nocturnal home ranges are 36.4 km^2 ($\bar{n} = 40$) and 28.1 km^2 ($\bar{n} = 28$), respectively.

contained the same number of permanent water sources as those constructed from daytime locations.

Use of vegetative associations was significantly different from availability during both diurnal and nocturnal periods ($P < 0.001$, both cases). Selection or avoidance of vegetative types was consistent between day and night for 6 of the 8 associations occurring within the study area (Table 5). Use of the triangleleaf bursage-foothills association was significantly greater during daytime compared to nighttime ($P < 0.05$). Disturbed sites were used in a significantly greater proportion at night than during the day ($P < 0.01$).

Table 5. Use of vegetation associations by female desert mule deer in the Belmont and Bighorn mountains, Arizona, 1990.

Vegetation Association	% of area	Day	Night
		% of locations (n=319)	% of locations (n=198)
Triangleleaf bursage- Brittlebush	1	5	3
Trinagleleaf bursage- Brittlebush Foothills	3	3	1
Triangleleaf bursage- Brittlebush Volcanic	6	27	29
Triangleleaf bursage- Brittlebush Transition	3	11	11
Creosote Flats	79	37	39
Disturbed Sites	2	1	4
Triangleleaf bursage- Palo-verde Northeast	3	4	4
Triangleleaf bursage- Palo-verde Southwest	3	12	10

DISCUSSION

Desert mule deer do not appear to be adapted behaviorally to desert conditions (Leopold and Krausman 1987, Anthony 1972). Potential behavioral adaptations include displacement or reduction of activity in high ambient temperatures, large home ranges, movement towards sources of water during dry periods, and use of habitat (or microhabitat) for thermoregulation. The results of this study indicate that desert mule deer alter activity patterns at certain times of the year. Home ranges are large ($\bar{x} = 32.3\text{km}^2$ for the 5 females used in the analysis) but do not expand to include more water sources during hot and dry periods.

Activity

In western Arizona, periods of high ambient temperatures occur throughout much of the year. Long-term escape from heat and aridity is not always possible. The combination of high temperatures and lack of moisture may affect the behavior of deer. Deer were least active diurnally and most active at night during spring, when temperatures were high and rainfall was most scarce. Desert mule deer appear to alter their daily activity cycle under the most extreme desert conditions.

Previous studies have shown nocturnal activity to peak during crepuscular hours for both white-tailed deer

(Montgomery 1963, Kammermeyer and Marchinton 1977) and mule deer (Eberhardt et al. 1984). My data indicate an increase in activity within the hour preceding sunrise in all seasons, and highest activity during the hour after sunset in 3 seasons. The 1 exception was spring, when temperatures recorded during the hour after sunset remained high (\bar{x} = 27.1 C). Although temperatures just after sunset were even higher in summer, there was also an increase in rainfall during this season (14.9 cm vs. 0.2 cm in spring). Visual observations of deer close to water were most frequent during the summer. All 5 observations of deer <400 m from water during this season occurred near intermittent water sources.

Nocturnal activity lulls were associated with crepuscular peaks. In Pennsylvania, white-tailed deer bedded most frequently 4-8 hours after sunset (Montgomery 1963). In Georgia, Kammermeyer and Marchinton (1977) found similar inactivity periods that occurred slightly earlier in the night (2200-midnight). Mule deer in Washington moved the shortest distances from midnight-0200 (Eberhardt et al. 1984). In this study, activity lulls were observed during each season, but these periods included midnight only during winter. Significant differences in activity during the 3 nighttime observation periods were found only in winter.

Predictions of activity rhythms based upon previous studies done in cooler climates held true only during winter. Although Montgomery (1963) concluded that daily activity patterns were largely determined by the ingestion-rumination cycle, there is evidence that environmental conditions had a notable effect. Ockenfels and Bissonette (1984) suggest that high ambient temperatures affect the behavioral patterns of white-tailed deer. Maghini and Smith (1990) reported that white-tailed deer in southwest Arizona visited water more frequently in hot-dry seasons than in hot-wet seasons. Columbian black-tailed deer in California are also reported to alter behavior outside a range of ideal ambient temperatures (Taber and Dasmann 1958).

Additional factors have been reported to influence deer activity. Increased feeding by deer during full moon nights is a common belief of hunters (Kufeld et al. 1988) and has been reported by some authors (Buss and Harbert 1950, Cowan 1956). Other studies suggest that moon phase has no effect on the nocturnal activity of mule deer (Kufeld et al. 1988) or white-tailed deer (Michael 1970, Zagata and Haugen 1974, Beier and McCullough 1990). Kie et al. (1991) found that moon phase did not influence the time mule deer spent foraging. No effect was observed in the Belmont and Bighorn mountains.

Kufeld et al. (1988) also reported no difference between cloudy and clear full-moon nights. The effect of cloud cover interacts with temperature and relative humidity, and varies with seasons (Beier and McCullough 1988). Any influence of cloud cover on nocturnal activity is probably indirect and related to its effect on diurnal activity.

Both Truett (1972) and I observed sharply reduced activity of mule deer during the hottest days of the year in Arizona. A corresponding increase in nocturnal activity of desert mule deer occurred. However, patterns of nocturnal activity could not be predicted solely by ambient temperature or other characteristics of the physical environment. The imperfect relationship between increased nocturnal activity and decreased diurnal activity suggests that total activity levels vary between seasons. Total activity could be affected by forage availability, forage quality, reproductive behavior, and other factors which change over the course of a year. Activity of desert mule deer in Arizona appears to reflect loose constraints of ruminant physiology that are modified according to particular environmental conditions.

Home Range

One possible behavioral adaptation of mule deer for

desert survival is a large home range. The 5 females from the Belmont and Bighorn mountains (\bar{x} = 20 cm rainfall/yr) used in the analysis had mean home range sizes of 32.3 km² using the MCP estimate. Home-range sizes are large compared to those of other nonmigratory mule deer in eastern Montana (\bar{x} annual precipitation = 28.7 cm) and southwestern Texas (\bar{x} annual precipitation = 28.5 cm). Mule deer in these areas had home ranges of 6.3 km² (Wood et al. 1989) and 3.8 km² (Dickinson and Garner 1979), respectively. In both of these studies, permanent water sources were distributed throughout the study area, and would likely be encountered by deer during the course of normal movements. Compared to other arid environments, home ranges in the Belmont and Bighorn mountains were similar in size to those in south-central Washington (\bar{x} annual precipitation = 16 cm, home range size = 31 km²) (Eberhardt et al. 1984), but smaller than home ranges of nonmigratory females in southwestern Arizona (\bar{x} annual precipitation = 11.4 cm, home range size = 121 km²) (Rautenstrauch and Krausman 1989). In the latter 2 studies, the few permanent water sources within the area were generally found on the periphery of the deer's home ranges. These results support the hypothesis that mammals have larger home ranges in more arid environments.

Movement and Habitat Use

Increased nocturnal movements during spring and summer may reflect a temporal displacement of daily movements, especially in conditions where daytime movements are suppressed as described by Truett (1972) for southeastern Arizona. Movement to water could be another source of additional nocturnal movements during spring and summer. Coues white-tailed deer (O. v. couesi) in southern Arizona moved outside diurnal ranges when summer-dry season home ranges did not contain a permanent water source (Maghini and Smith 1990). Although deer in the Belmont and Bighorn mountains did not migrate outside diurnal home ranges to find drinking water, visits to water sources within a deer's home range would be expected to increase in frequency during hot and dry periods. Nine of the 13 visual [daylight] locations of deer observed <400 m from sources of water occurred within 2 hours of sunrise or sunset. This suggests that movements to water sources are 1 component of the increased movement distances observed during spring and summer.

I expected greater movement distances at the beginning (sunset-2159) and end (0200-sunrise) of the night based on previous research. Smaller movement distances would be expected to coincide with the activity

lulls occurring around midnight reported by Montgomery (1963) for white-tailed deer and by Eberhardt et al. (1984) for mule deer. I found movement distances to be smaller in the middle (2200-0159) of the night than at the beginning, but the differences were not significant, possibly due to the limited precision of the techniques used for nighttime locations. Further research with more precise locational techniques would be required to identify movement lulls in the middle of the night, and to determine if shorter movements coincide with the apparent activity lulls occurring about 0200 hours.

Patterns of nighttime habitat use generally followed those found during the day. In this area, daytime locations should be sufficient to generate accurate habitat use data. The 1 exception might be the increased use of disturbed sites at night. Although the frequency of potential disturbances is relatively low along the CAP even during the daytime, these areas were used significantly more at night when nearby vehicular traffic was virtually nonexistent. This pattern could reflect an avoidance of human disturbances, as suggested by Montgomery (1963). Vogel (1989) found increased nocturnal activity of deer in areas of greater housing densities and therefore greater potential disturbance. Other factors may also contribute to the use of disturbed

sites at night. The areas just north of the CAP had significantly more green vegetative cover than the surrounding areas due to water backup along the CAP (P. R. Krausman, Univ. Ariz., unpubl. data). Increased nocturnal activity in these areas of high forage availability parallels McCullough's (1982) observations of activity and habitat use of white-tailed deer in Michigan during spring.

MANAGEMENT IMPLICATIONS

Although it has been recommended that nighttime locations be obtained when describing use of water sources or areas of variable topography, it is rarely done in studies that utilize aerial locations (Miller et al. 1984). Visits to water sources by desert mule deer are most common at night, especially at sunset (Hervert and Krausman 1986). Studies of desert mule deer behavior at water sources would require nocturnal observations, but this study suggests that use of water sources can be accurately determined from daytime locations. Diurnal home ranges included or were directly adjacent to all water sources found within nocturnal home ranges in this study. Nocturnal movements to water in the Bighorn and Belmont mountains do not appear to lead deer outside of their diurnal home ranges.

General patterns of nocturnal habitat use were accurately represented by daylight observations. Selection or avoidance of the 6 most common vegetation associations did not change significantly between day and night. However, use of disturbed sites was under-represented by daytime locations. This may be analogous to an observed increase in nocturnal activity of mule deer with higher housing densities reported by Dasmann and Taber (1956) and Vogel (1989). Potential influences

of human disturbance on habitat use should be considered when selecting times to observe mule deer. For more pristine areas such as the Belmont and Bighorn mountains, daytime locations are sufficient to represent overall patterns of habitat use.

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