Factors Affecting Habitat Use and Distribution of Desert Mule Deer in an Arid Environment

JASON P. MARSHAL,[1,2] *School of Natural Resources, University of Arizona, Tucson, AZ 85721, USA*

VERNON C. BLEICH, *Sierra Nevada Bighorn Sheep Recovery Program, California Department of Fish and Game, Bishop, CA 93514, USA*

PAUL R. KRAUSMAN, *School of Natural Resources, University of Arizona, Tucson, AZ 85721, USA*

MICKEY LYNN REED, *School of Natural Resources, University of Arizona, Tucson, AZ 85721, USA*

NANCY G. ANDREW, *California Department of Fish and Game, Bermuda Dunes, CA 92201, USA*

Abstract

*We studied habitat use by desert mule deer (*Odocoileus hemionus eremicus*) in the Sonoran Desert to understand the relative importance of vegetation, terrain characteristics, human disturbances, and water sources in determining their distribution. We located 44 radiocollared female mule deer weekly over 5 years. In spring, when water was most scarce, deer were in areas with lower elevations, shallower slopes, and greater normalized difference vegetation index (NDVI) rates, when compared to random locations. Use of water developments (i.e., catchments) during spring was evident but their effect on deer distribution was small relative to other factors, and their importance varied by animal. More deer locations were recorded in areas of higher NDVI rate in spring, summer, and autumn, but they were also further from washes in autumn. The deer we monitored used lower elevations in spring and higher elevations during the rest of the year. The effect of slope was strong in all seasons. However, deer tended to select shallow slopes in spring and steep slopes during the rest of the year. Deer avoided roads in summer and autumn but were closer to them in winter. They avoided rivers or canals in summer but were closer to those features in autumn. Our results suggest that terrain characteristics in all seasons (slope and elevation), as well as forage quality in 3 of 4 seasons (as indexed by NDVI rate) were most important in determining distribution of deer. Concomitantly water catchments had a measurable, but minor, role during hot, dry conditions. We recommend investigators continue to evaluate the importance of water developments relative to other habitat factors, particularly via the use of multivariate studies, global positioning system technology, adaptive management, and temporary closure of water developments known to be used by radiocollared deer. (WILDLIFE SOCIETY BULLETIN 34(3):609–619; 2006)*

Key words

Management of wildlife populations requires continuing efforts to understand the interactions between wildlife species and their habitats. In their simplest form, habitat studies describe the general distribution of animals (Morrison 2001), that is, where animals occur and the characteristics of their environments. However, such studies frequently fail to reveal widely applicable relationships because they do not address the underlying causal patterns between environmental factors, particularly resources that support animals and the demographics of those animals (Morrison 2001). It is the understanding of these underlying relationships that allow predictions about occupancy, abundance, survival, and reproduction in wildlife populations (Hobbs and Hanley 1990).

Treating habitat studies as an investigation of an animal's niche provides the causal link between a species and factors that affect it (Morrison 2001). In this context the resources and conditions that make up an animal's habitat are treated as niche parameters. Of several resources that could determine the distribution of desert animals, those commonly considered for mule deer are availability of forage (Albert and Krausman 1993, Marshal et al. 2005*a*), nutritional quality of forage (Rautenstrauch et al. 1988, Albert and Krausman 1993, Marshal et al. 2005*b*), cover (Ordway and Krausman 1986), mating sites (Scarbrough and Krausman 1988), natal sites (Fox and Krausman 1994), and sources of water (Hervert and Krausman 1986). Several environmental conditions

[1] *E-mail: jmarshal@ualberta.net*
[2] *Present address: Campbell River, BC V9H 1A6, Canada*

also may influence distribution of mule deer, such as sources of human disturbance (e.g., roads, mines; Krausman 1998) or terrain characteristics (e.g., elevation, slope; Ordway and Krausman 1986). An understanding of these niche parameters and their relative importance in affecting mule deer distribution allows wildlife managers to make predictions about occupancy and impacts of alteration to habitat.

Desert mule deer (*Odocoileus hemionus eremicus*) occur in Imperial County, California, USA, and there have been few studies (e.g., Blong 1993, Thompson and Bleich 1993) to contribute information for the management of these animals in that geographic area. They experience a variety of influences, many of them human-caused, which may have the potential to detrimentally affect mule deer populations (e.g., harvest, alteration of habitat, recreational use). Some research and management efforts have occurred in the past, primarily through the provision of water via catchments, but their effects on the deer of this region have not been studied. In an effort to develop a better understanding of habitat use for these animals, our objective was to study the factors that influence distribution of mule deer across a desert landscape and, in particular, the role of water catchments as one of these factors.

Study Area

We conducted this study from May 1999 to June 2004 in the Lower Colorado River Valley subdivision, Sonoran Desert, Imperial County, California, USA (33°00′N, 114°45′W; Fig. 1). Range in elevation was sea level to 644 m at Quartz Peak.

Figure 1. Study area in eastern Imperial County, California, USA.

Figure 2. The Cargo Muchacho Mountains, Imperial County, California, USA. Most plant biomass occurred along washes; little vegetation occurred outside these zones.

Temperatures in summer were frequently >45°C and were rarely below freezing in winter. Annual precipitation in nearby Imperial Valley, California, USA, was low on average (74 mm) but highly variable (range 4–216 mm; 1914–2003, Imperial Irrigation District, unpublished data). The approximate size of the study area was 1,100 km². Major landforms were mountain, piedmont (rolling hills), and flats (Andrew et al. 1999). Each landform contained washes (11% of study area) and desert pavement (i.e., a naturally occurring, smooth cobble rock surface). Washes were streambeds that remained dry during most of the year but had flowing water during rainstorms of sufficient intensity. More than 90% of plant biomass was in narrow (≤5 m) xeroriparian zones following the banks of washes (Marshal et al. 2005a). Little vegetation occurred outside xeroriparian zones (Fig. 2; Andrew 1994).

Turner (1994) described the vegetation associations of the Lower Colorado Region in general and Andrew (1994) described those for our study area in particular. Common plants in mountainous areas were creosote bush (*Larrea tridentata*), burro-weed (*Ambrosia dumosa*), brittle-bush (*Encelia farinosa*), and ocotillo (*Fouquieria splendens*; Andrew 1994). Piedmont and flats contained creosote bush, burro-weed, brittle-bush, blue palo verde (*Parkinsonia florida*), and matchweed (*Gutierrezia microcephala*; Andrew 1994). In washes catclaw (*Acacia greggii*), desert ironwood (*Olneya tesota*), and cheese bush (*Hymenoclea salsola*) were common. Cholla and prickly pear (*Opuntia* spp.) and creosote bush occurred in low abundance outside washes (Andrew 1994).

Several water sources were available to deer in the study area. The Colorado River flowed along the east side of the study area (Fig. 1). An agricultural canal (the All-American Canal) formed part of the southeastern and southern boundary of the study area. To the east of Ogilby Road were 17 wildlife water developments (i.e., catchments) at an average density of 1/35 km². There also

were natural rock basins and springs, most of which became dry during the hot, dry season. During the course of this study, 4 additional catchments were constructed as routine management actions at the periphery of the study area. Because water already was available in the study area, their influence was presumed to be minimal.

We defined seasons according to behavior of the deer and their responses to seasonal variation in rainfall and temperature. Winter (cool, rainy) began around 1 January with the beginning of rut. Spring (hot, dry) began when deer moved to within 5 km of catchments during April or May. Summer (hot, rainy) began July–September when the first monsoon rains occurred and deer moved to >5 km from catchments and spread out across the study area. Autumn (cool, dry) began around 1 October after the last summer rains. Seasons were variable between years, and they almost never began on the same dates in different years (Table 1).

The mule deer in this region typically exhibit low densities (Thompson and Bleich 1993). During this investigation, density in the study area fluctuated between 0.05 and 0.13 deer/km² (Marshal et al. 2006). Other large- and medium-sized herbivores in the area were bighorn sheep (*Ovis canadensis*), feral ass (*Equus asinus*), black-tailed jackrabbit (*Lepus californicus*), desert cottontail (*Sylvilagus audubonii*), and desert tortoise (*Gopherus agassizii*). Potential predators of deer included mountain lion (*Puma concolor*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), and golden eagle (*Aquila chrysaetos*; Andrew et al. 1997a). Hunting season occurred in October and November, and 15–60 male deer were removed each year from the hunt zone that included our study area; about half of those came from the study area itself.

Methods

Deer Capture and Monitoring

All aspects of this research complied with acceptable field methods adopted by the American Society of Mammalogists (Animal Care and Use Committee 1998) and followed standard California Department of Fish and Game (CDFG) protocols for animal handling and safety (Jessup et al. 1986).

We captured mule deer with a net gun fired from a helicopter (Krausman et al. 1985a). Deer were hazed into open areas to

Table 1. Dates of seasons based on behavior of radiocollared mule deer and their responses to changes in rainfall and temperature, plus associated rainfall (mm) from nearby Imperial Valley, Imperial County, California, USA, 1999–2004.

	Winter		Spring		Summer		Autumn	
	Dates	Rainfall	Dates	Rainfall	Dates	Rainfall	Dates	Rainfall
1999			13 Apr–9 Jul	0	10 Jul–15 Oct	32	16 Oct–22 Dec	0
2000	23 Dec–26 Mar	7	27 Mar–22 Aug	0	23 Aug–15 Oct	16	16 Oct–9 Jan	1
2001	10 Jan–22 Jun	42	23 Jun–6 Jul	0	7 Jul–30 Sep	0	1 Oct–13 Jan	0
2002	14 Jan–22 May	0	23 May–8 Sep	0	9 Sep–6 Oct	11	7 Oct–31 Dec	7
2003	1 Jan–22 May	39	23 May–31 Jul	0	1 Aug–31 Sep	26	1 Oct–31 Dec	4
2004	1 Jan–31 May	60	1 Jun–28 Jul	1				

facilitate capture. Chase time for any animal was <5 minutes. Upon capture, the crew blind-folded and hobbled the deer to facilitate handling and protect the animal (Jessup et al. 1986). We attached a radiocollar with 6-hour-delay mortality signal (Telonics MOD-500, Mesa, Arizona) and released the deer.

To locate deer we flew approximately weekly with a fixed-wing aircraft carrying 2 H-type antennas, one on each wing. The aircraft flew at 180 km/hour, 300 m above ground level, while we scanned through the collar frequencies. When we identified a collared deer, we slowed the aircraft and circled until we achieved the strongest possible signal (Krausman et al. 1984). For safety reasons, we did not fly low enough to attempt visuals (Bleich et al. 2001). When we had an accurate location, we recorded it in degrees latitude and longitude on a global positioning system (GPS) receiver (Garmin GPS 12XL, Olathe, Kansas). We later downloaded the geographic coordinates directly to computer for analysis. We measured the accuracy of this method by locating radiocollars placed at known ground locations; the pilot and data recorder were unaware which collars were on animals and which were for measuring accuracy.

Data Analysis

Habitat model.—We developed habitat models for mule deer using geographic information system (GIS) models of landscape features. We used ARC/INFO software (Environmental Systems Research Institute, Redlands, California) to develop the habitat models. The GIS component consisted of raster-based models of terrain attributes, distances to features, and vegetation indices. We used 7 GIS layers to represent resources or habitat components in our study area, each with an extent sufficient to cover the study area. Sources of data for this analysis were the California Spatial Information Library (http://gis.ca.gov/) and GIS Data Depot (http://data.geocomm.com/).

Elevation was estimated from a 30-m-resolution United States Geological Survey (USGS) digital elevation raster model. We used this layer to derive slope. We developed a distance-to-roads layer from an existing line-vector road coverage for Imperial County. To develop a distance-to-wash layer, we digitized a polygon wash layer from 1-m-resolution digital satellite photos (USGS digital orthographic quarter quadrangles [DOQQ]) of the study area. We measured locations of catchments with a GPS unit and entered them into a point-vector layer. We used a distance-to-river layer that included the Colorado River and the All-American Canal. This layer came from an existing polygon-vector coverage of rivers and canals for California. For each

"distance-to" layer, we converted each vector model into a 30-m raster model and then calculated the distances from the center of each cell to the center of those containing the feature represented in the original vector layer.

We used a vegetation index in our habitat model, derived from the normalized difference vegetation index (NDVI), which correlates greenness values with primary productivity of an area (Parker 2003). For example, Griffith et al. (2002) used NDVI and NDVI rate (i.e., the differences between consecutive NDVI images) as indices to forage biomass and quality, respectively, for caribou (*Rangifer tarandus*) in Alaska, USA. We used biweekly NDVI images, having a resolution of 1 km, to calculate NDVI rate as a location-specific index to forage quality. Preliminary analysis demonstrated a greater ability for NDVI rate to predict deer distribution; therefore, we did not include the original NDVI layers in the habitat model. The NDVI layers used in our model had been converted from the standard 0–1 value range for land surfaces to an 8-bit color scale, to conserve computing resources; thus, the values from the NDVI images were integers without units that ranged from 0–200 (Wallace 2002). Typical values from our study area, however, were narrower than this (approx. 100–150). The NDVI rate layers were differences between consecutive images, so their values could be positive or negative, depending on whether the value for a particular pixel increased or decreased between biweekly periods. Because deer locations were date-specific, we associated each location with the appropriate biweekly NDVI rate layer. Efforts to relate NDVI imagery to vegetation characteristics in some desert areas, including our study area, have met with limited success (Wallace 2002, J. P. Marshal et al., University of Arizona, unpublished data). Use of this imagery was based on our assumption that it reflected the forage characteristics found in our study area.

Resource selection analysis.—We used logistic regression to evaluate the influence of environmental factors on distribution of mule deer (Manly et al. 2002). We considered habitat selection at 2 spatial scales: that at which it influenced animal locations within the home range (Johnson's [1980] third-order selection), and that at which selection influenced the location of the home range within the population range (Johnson's [1980] second-order selection).

For placement of animal location within home range (i.e., within-home-range analysis), we identified seasonal home ranges for each deer using the minimum convex polygon (MCP; Mohr 1947). We evaluated whether there was a sufficient number of locations per animal by determining the sample size at which there

was no longer a substantial change in home-range size as deer locations were added at random (Mares et al. 1980). We set the number of locations at which there was no substantial change as occurring when the 95% confidence intervals for the average change in home-range size included 0. We conducted this evaluation separately by season.

For each season and animal where our data requirements were met, we determined the MCP seasonal home range (across years), and generated a sufficient number of random locations to cover the area within the home range (approx. 3–4 times the no. of deer locations). We then buffered observed and random locations by an amount estimated in this study to account for telemetry accuracy. We used ARC/INFO to associate each location with the average value within the buffer for each GIS layer. These averages became the data that we used to analyze deer distribution in logistic regression analyses. For analysis of home-range location within the study area (i.e., within-study-area analysis), we compared mean values of the GIS layers within observed home ranges to randomly placed, circular home ranges of a size equal to the observed seasonal average (Katnik and Wielgus 2005). We selected a sufficient number of random home ranges to cover areas defined by seasonal MCP polygons that contained the locations of all radiocollared deer for each season (approx. 3 times the no. of observed home ranges). We then used the mean values generated for each GIS layer within the random and observed home ranges in a logistic regression analysis.

We used the information-theoretic approach based on Akaike's Information Criterion (AIC) to fit logistic regression models (Burnham and Anderson 2002). We developed 2 sets of candidate models (one for each scale of analysis) from 2 full models. The full model for the within-home-range analysis contained the variables elevation, slope, NDVI rate, and distances to roads, washes, water developments, and the canal or river. Because of sample-size constraints, we did not estimate separate seasonal MCP home ranges for each year. As a consequence, the full model for the within-study-area analysis did not include NDVI rate because the NDVI images are date specific and vary over biweekly periods. As a result we believed it inappropriate to use averages across biweekly periods within or across years.

We used a use–availability design and, hence, we were limited to estimating a logistic discriminant function rather than a resource selection function (Keating and Cherry 2004). A discriminant function would allow us to evaluate the relative effects of explanatory variables on distribution of deer, but it would not allow us to develop a reliable function for predicting likelihood of use (Keating and Cherry 2004). For the within-home-range analysis, we developed functions separately for each animal and each season. In some instances we had small sample sizes relative to the number of variables in our models; consequently, we used the small-sample AIC (AIC_c) for model selection (Burnham and Anderson 2002). Individual functions were the average of fitted models from the set of candidates, using Akaike weights to influence the contribution of a particular candidate model according to its likelihood of being the best of the candidates (Burnham and Anderson 2002). From the model-averaged individual functions, we estimated 4 overall seasonal functions based on the average of coefficients for each variable across individual deer (Boyce and Waller 2003) weighted by observations per individual. We used bootstrap methods to estimate variation in coefficients among deer (Manly et al. 2002) and to calculate 95% confidence intervals. We used similar methods to fit seasonal logistic regression models for the within-home-range analysis, except that no averaging of coefficients across individuals occurred.

The inferences we made based on these coefficients and their confidence intervals were design-based rather than model-based (Manly et al. 2002), meaning observed variation was based on differences in model coefficients among deer, rather than on fit of data from individual deer to a particular model. Because variables for these models were selected by information-theoretic methods instead of hypothesis tests, the confidence intervals did not reflect statistical significance of the explanatory variables in the conventional sense. We judged the strength of the average effect from the absolute value of the coefficient. If both bounds of the confidence interval were above or below 0, we concluded that habitat component had similar influence on all deer in our sample (i.e., the effect was consistent). In some cases the confidence interval tended to one side of, but contained, 0. In this instance, we concluded the habitat component tended to be important for most deer, but that there was some variability in its effect among deer. Finally, there were instances where the confidence interval was approximately symmetrical around 0. In this case we concluded that importance of that component was variable among deer (i.e., for some deer there was evidence for selection, for some avoidance, and for some it was unimportant).

Results

We captured 44 female mule deer to conduct this study. Minimum number of locations for a winter home range was 40 ($n = 11$ deer met this requirement), 25 ($n = 18$) for spring, 11 ($n = 28$) for summer, and 33 ($n = 10$) for autumn (Table 2). Number of observations of deer ranged from 396 in autumn to 570 in spring (Table 2). Based on 32 known-location telemetry observations, average telemetry error was 380 m (95% CI: 308–451). To be certain that we were accounting for the largest likely uncertainty in telemetry locations, we used a 500-m buffer in our GIS analysis.

Within-Home-Range Analysis

Our resultant functions indicated that 3–6 explanatory variables were useful for distinguishing between random and observed use, depending on season (Tables 3–6). For spring, these were locations of catchments, elevation, NDVI rate, and slope (Table 3). Of the factors that had an influence on deer distribution in spring, locations of catchments had the smallest effect, and its importance was variable among deer. Elevation had the next largest effect, where observed use was associated with lower-elevation areas, on average, than random use; this effect was relatively consistent among deer. Locations of deer were associated with areas of greater NDVI rates and shallower slopes than random locations; the effect of NDVI rate was variable among deer, whereas observed use was consistently associated with shallower slopes than was random use.

In summer all explanatory variables appeared to contribute to distinguishing observed from random locations: distances to catchment, river or canal, roads, and washes; elevation; NDVI

Table 2. Number of home ranges, observed locations, and random locations used in the habitat analysis of radiocollared mule deer, Imperial County, California, USA, 1999–2004.

Season	No. home ranges	Observed locations	Random locations
Spring	18	570	1,710
Summer	28	544	1,632
Autumn	10	396	1,188
Winter	11	490	1,470

rate; and slope (Table 4). Distance to river and roads had the weakest effects, with observed use being associated with locations further from these features than random use, and their effects were consistent among deer for roads but variable for river. On average, observed use was consistently associated with areas of greater NDVI rate and further from washes than random. Observed use was on steeper slopes and at higher elevations than random, but their influences were variable. Distance to catchments had a small and variable effect, with observed locations occurring on average further from catchments than did random locations.

During autumn, observed and random use were distinguished primarily by distances to the river or canal, roads, and washes; elevation; NDVI rate; and slope (Table 5). Slope and NDVI rate had the largest effects, where observed use was associated on average with greater NDVI rates and steeper slopes than random use; these influences were variable among deer for NDVI rate but consistent for slope. Distances to river or canal, washes, and roads, and elevation each had smaller effects; observed locations were associated with higher elevations, areas further from washes and roads, and closer to the river than random locations. The influences of roads, the river, and elevation were variable, but the influence of washes was more consistent among deer.

During winter, observed use was distinguished from random use by distances to roads and washes, elevation, and slope (Table 6). The strongest effect was for slope, where observed locations were associated with steeper slopes, but these influences varied among deer. Observed locations were associated with lower elevations and areas further from washes, but these factors had smaller overall effects. The effect of roads was also small: deer were closer to roads than random locations, but the effect varied among deer.

In summary, deer use within home range could be distinguished from random locations by elevation and slope throughout the year. Distinguishing features for spring (hot dry) included distance to catchments and NDVI rate. For summer (hot rainy), these were distances to catchments and washes, as well as NDVI rate. In

autumn (cool dry), distances to river, roads, and washes, and NDVI rate were important in distinguishing observed from random use. By winter (cool rainy), distances to roads were important.

Within-Study-Area Analysis

For all home ranges, degree of selection and importance of factors varied among deer (Table 7). Nonetheless, in all seasons deer tended to have home ranges at higher elevations than random home ranges. In spring and summer, observed home ranges were on shallower slopes, and in autumn they were on steeper slopes. There was a small effect of distance to river or canal in summer, autumn, and winter, where deer home ranges were further from these features than random home ranges. There was also a small effect of distance to catchment on locations of observed home ranges in autumn. Observed home ranges appeared closer to roads in autumn and winter. There was also a small effect of distance to washes in autumn, with observed home ranges occurring closer than random home ranges.

Discussion

Efforts to understand interactions between wildlife and their habitats require an understanding of the resources or environmental conditions that promote the occupancy of an environment, as well as factors that may constrain the influences of those resources or conditions. In the present study, we considered several resources: vegetation as available from riparian associations in the study area, forage (via NDVI), and water. Conditions may be influenced by vegetation associations, elevation, and slope, all of which may alter microclimate by influencing exposure or variation in temperature. Roads may be a potential constraint on the use of other habitat components as a source of human disturbance, or they may facilitate use of other resources as corridors.

Influence of Habitat Components

We found support in our results for the notion that forage characteristics are important components of habitat. Our index of forage quality, NDVI rate, was important in influencing deer distribution in our within-home-range models in 3 of 4 seasons. Except for winter, observed use was associated with greater NDVI rates than random locations. Winter may have been an exception because, during this season, much of the desert has relatively abundant, high-quality forage. This also is the season during which rut occurs. Locations of deer at this time may have been influenced by factors other than forage quality.

A proportional relationship between forage growth (or quality)

Table 3. Mean coefficients, bootstrapped standard errors, and 95% lower and upper confidence limits (LCL and UCL) of model-averaged logistic functions discriminating between observed and random use within home ranges of mule deer in spring, Imperial County, California, USA, 1999–2004.

Variable	Mean	SE	95% LCL	95% UCL	Compared to random locations, deer were...
Distance to catchment	−0.000014	0.000010	−0.000035	0.000005	closer to catchments
Distance to river or canal	0.000005	0.000007	−0.000010	0.000019	similar for the river or canal
Distance to roads	−0.000007	0.000043	−0.000080	0.000085	similar for roads
Distance to washes	−0.000054	0.000196	−0.000369	0.000337	similar for washes
Elevation	−0.001932	0.000705	−0.003553	−0.000691	at lower elevations
NDVI rate[a]	0.002988	0.005653	−0.007616	0.013342	with greater rates of NDVI change
Slope	−0.013040	0.007285	−0.029669	−0.001318	on shallower slopes

[a] Normalized Difference Vegetation Index rate = difference between consecutive NDVI layers.

Table 4. Mean coefficients, bootstrapped standard errors, and 95% lower and upper confidence limits (LCL and UCL) of model-averaged logistic functions discriminating between observed and random use within home ranges of mule deer in summer, Imperial County, California, USA, 1999–2004.

Variable	Mean	SE	95% LCL	95% UCL	Compared to random locations, deer were...
Distance to catchment	0.000022	0.000015	−0.000009	0.000052	further from catchments
Distance to river or canal	0.000006	0.000008	−0.000011	0.000021	further from the river or canal
Distance to roads	0.000154	0.000048	0.000071	0.000258	further from roads
Distance to washes	0.000198	0.000161	0.000097	0.000516	further from washes
Elevation	0.000555	0.000666	−0.000779	0.001823	at higher elevations
NDVI rate[a]	0.004178	0.002085	0.000003	0.008124	with greater rates of NDVI change
Slope	0.011141	0.007205	−0.001222	0.027052	on steeper slopes

[a] Normalized Difference Vegetation Index rate = difference between consecutive NDVI layers.

and NDVI rate must be assumed for this area. Relationships between forage growth and forage nutritional quality for deer have been demonstrated for this study area (Marshal et al. 2005*b*). However, we must rely on relationships established in other environments (e.g., Tucker and Sellars 1986) to make inferences about forage characteristics from NDVI imagery. Efforts to establish relationships between NDVI and plant characteristics have met with limited success in the present study area, perhaps because most of this desert landscape is free of plant biomass (Andrew 1994, Marshal et al. 2005*a*). Wallace (2002) used similar imagery to develop habitat models for elk (*Cervus elaphus*) and pronghorn (*Antilocapra americana*) in semiarid and arid regions of Arizona.

Despite these limitations, the most plausible explanation for the associations between NDVI rate and observed use by deer is that NDVI rate reflected forage quality. Distribution of herbivores is strongly influenced by availability of nutrients in the environment. Among red deer (*Cervus elaphus*) in an experimental pasture, distribution of feeding time among patches was closely related to intake rates of protein in those patches (Langvatn and Hanley 1993). Movements of free-ranging wildebeest (*Connochaetes taurinus*) occurred in response to changes in the condition of grass resources; smaller-scale movements appeared to be in response to localized rains causing ephemeral growth in green forage (Wilmshurst et al. 1999). White-tailed deer (*Odocoileus virginianus*) foraged predominantly in patches of new growth containing shrub sprouts of higher nutritional quality, in comparison to areas containing mature shrubs and lower-quality forage (Stewart et al. 2000). These examples from different systems demonstrate the importance of high-quality, rapidly growing forage in determining distribution of large herbivores and also the likely importance of forage quality (as indexed by NDVI rate) in determining distribution of deer in our study area.

Our results with respect to washes were unexpected. During winter and spring, distribution of observed and random locations was similar. For the other seasons, however, deer locations tended to be further from washes than random locations. This was counterintuitive, considering that washes were the only source of forage and cover in this study area, a pattern common to many desert systems (Krausman 1998). Previous work in this area showed use for washes and their associated vegetation throughout the year (Blong 1993). Desert mule deer were also located in washes in 71% of observations in the Belmont Mountains, Arizona, and in >99% of observations in King Valley, Arizona, USA (Krausman et al. 1985*b*). A factor that may have contributed to this result may have been the size of washes deer select compared to the size of washes easily visible on a 1-m-resolution DOQQ image. Washes we digitized from these images probably reached sizes as small as 5 m wide (because of the difficulty of identifying and accurately digitizing washes narrower than 5 m), but many washes in our study area could have been smaller than this. Thus, our distance-to-wash layer actually may have reflected distance to large washes, and avoidance or random use may have been with respect to these larger washes. Perhaps there was selection for smaller washes and avoidance of larger washes, related to avoidance of predators or human disturbance. Also, smaller washes with lower biomass may have had higher rates of plant growth (Marshal et al. 2005*a*) and, thus, higher-quality forage (Marshal et al. 2005*b*). As a result selection of smaller washes by deer may have been related to the forage quality found in those washes.

Elevation and slope were important in the within-home-range models for all seasons, but their influences varied with season. Summer and autumn locations were associated with higher elevations, and spring and winter locations were associated with lower elevations. These patterns may be the result of behaviors associated with birthing. Births generally occur in summer, after

Table 5. Mean coefficients, bootstrapped standard errors, and 95% lower and upper confidence limits (LCL and UCL) of model-averaged logistic functions discriminating between observed and random use within home ranges of mule deer in autumn, Imperial County, California, USA, 1999–2004.

Variable	Mean	SE	95% LCL	95% UCL	Compared to random locations, deer were...
Distance to catchment	0.000004	0.000008	−0.000013	0.000018	similar for catchments
Distance to river or canal	−0.000008	0.000005	−0.000019	0.000001	closer to the river or canal
Distance to roads	0.000022	0.000036	−0.000044	0.000098	further from roads
Distance to washes	0.000642	0.000460	0.000019	0.001660	further from washes
Elevation	0.000426	0.000413	−0.000199	0.001381	at higher elevations
NDVI rate[a]	0.006031	0.005317	−0.004940	0.016052	with greater rates of NDVI change
Slope	0.016611	0.009356	0.000260	0.037303	on steeper slopes

[a] Normalized Difference Vegetation Index rate = difference between consecutive NDVI layers.

Table 6. Mean coefficients, bootstrapped standard errors, and 95% lower and upper confidence limits (LCL and UCL) of model-averaged logistic functions discriminating between observed and random use within home ranges of mule deer in winter, Imperial County, California, USA, 1999–2004.

Variable	Mean	SE	95% LCL	95% UCL	Compared to random locations, deer were...
Distance to catchment	−0.000002	0.000005	−0.000011	0.000008	similar for catchments
Distance to river or canal	0.000000	0.000004	−0.000007	0.000007	similar for the river or canal
Distance to roads	−0.000025	0.000017	−0.000058	0.000011	closer to roads
Distance to washes	0.000024	0.000074	−0.000113	0.000171	similar for washes
Elevation	−0.000658	0.000589	−0.001975	0.000031	at lower elevations
NDVI rate[a]	−0.000076	0.005680	−0.011639	0.009848	similar for NDVI rate
Slope	0.010337	0.008683	−0.004473	0.029762	on steeper slopes

[a] Normalized Difference Vegetation Index rate = difference between consecutive NDVI layers.

monsoon rains begin (Fox and Krausman 1994). Selection of higher elevation may be a strategy to avoid or evade predators (Bleich 1999) that may be attracted to vulnerable neonates. By winter, young-of-the-year were approximately 6 months old, at which time there were likely fewer sources of mortality and survival rates increased (Gaillard et al. 2000, Bleich et al. 2006). Presumably, young were less vulnerable to predation by this age, and dam–young groups could move to lower areas where predators were more abundant (Bleich et al. 1997), but where forage and cover in washes were greater (Andrew 1994, Marshal et al. 2005a). Ordway and Krausman (1986) found that montane regions of the Belmont range were used for birthing and rearing of young. They argued that this use reflected selection of regions with abundant forage, rather than of regions of higher elevation per se, to reduce predation risk. In our Imperial County study area, deer forage was relatively scarce in mountainous regions, compared to lower regions where washes were more common (Marshal et al. 2005a). However, other investigators have proposed that females may deliberately disperse from conspecifics and select mountainous areas in which to give birth. For example, caribou in British Columbia and Alaska selected areas of high elevation for birthing as a strategy to increase distance between themselves and predators in valley bottoms (Bergerud and Page 1987, Barten et al. 2001).

Based on observed habitat use during the birthing season, slope appears to have an important influence on selection of birthing habitat for mule deer. In our study, however, the influence of slope was unclear. Outside of spring there was a tendency for observed use to occur on steeper slopes, but there was substantial variation among deer. In the Belmont Mountains, Fox and Krausman (1994) reported higher incidence of coyote scat in less-steep areas, and they suggested that use of steep slopes may be a strategy to avoid coyote predation. This suggestion was echoed by Riley and Dood (1984), who associated fawn habitat with steep slopes, because coyotes tended to travel along ridge tops and valley bottoms; indeed, coyotes are much less common on steep slopes than in other areas (Bleich et al. 1997).

Table 7. Coefficients, standard errors, and 95% lower and upper confidence limits (LCL and UCL) for a logistic function discriminating between observed and random home ranges of mule deer, Imperial County, California, USA, 1999–2004. Coefficients are from averaged models, and model selection occurred separately for each season.

Season	Variable	Estimate	SE	95% LCL	95% UCL	Compared to random home ranges, observed home ranges were...
Spring	Distance to catchment	0.000000	0.000000	0.000000	0.000000	similar for catchments
	Distance to river or canal	−0.000004	0.000023	−0.000048	0.000041	similar for rivers or canals
	Distance to roads	0.000000	0.000000	0.000000	0.000000	similar for roads
	Distance to wash	0.000000	0.000000	0.000000	0.000000	similar for washes
	Elevation	0.001092	0.001728	−0.002296	0.004480	at higher elevations
	Slope	−0.023124	0.026931	−0.075909	0.029661	on shallower slopes
Summer	Distance to catchment	0.000000	0.000000	0.000000	0.000000	similar for catchments
	Distance to river or canal	0.000007	0.000022	−0.000035	0.000050	further from rivers or canals
	Distance to roads	0.000000	0.000000	0.000000	0.000000	similar for roads
	Distance to wash	0.000000	0.000000	0.000000	0.000000	similar for washes
	Elevation	0.000068	0.000073	−0.000075	0.000211	at higher elevation
	Slope	−0.023572	0.026350	−0.075218	0.028075	on shallower slopes
Autumn	Distance to catchment	−0.000014	0.000020	−0.000053	0.000025	closer to catchments
	Distance to river or canal	0.000009	0.000019	−0.000028	0.000046	further from rivers or canals
	Distance to roads	−0.000117	0.000285	−0.000676	0.000442	closer to roads
	Distance to wash	−0.000031	0.000037	−0.000103	0.000042	closer to washes
	Elevation	0.001220	0.001282	−0.001293	0.003734	at higher elevation
	Slope	0.013128	0.041893	−0.068982	0.095239	on steeper slopes
Winter	Distance to catchment	0.000000	0.000000	−0.000001	0.000000	similar for catchments
	Distance to river or canal	0.000012	0.000017	−0.000022	0.000046	further from rivers or canals
	Distance to roads	−0.000128	0.000289	−0.000695	0.000439	closer to roads
	Distance to wash	0.000000	0.000000	0.000000	0.000000	similar for washes
	Elevation	0.000136	0.000146	−0.000151	0.000422	at higher elevation
	Slope	0.001221	0.044504	−0.086007	0.088448	similar for slopes

Distance to roads had an influence on observed use in the summer, autumn, and winter within-home-range models. The roads layer we used included paved highways, maintained dirt roads, abandoned dirt roads, and 2-track off-road trails traveled mostly by local resource users. Consequently, degree of use and influence on deer likely varied by road type. During most of the year, vehicular traffic we observed was limited to paved highways and maintained dirt roads. Nonetheless, there was evidence that deer may have avoided roads in 2 seasons. In summer and autumn, deer were further from roads than were random locations, perhaps to avoid human disturbance or areas easily accessed by predators. Also, hunting season occurred in autumn. In general, however, overall effect of distance to roads was small when compared to other factors, and in winter its importance varied among deer.

Distance to river or canal generally was only an influence on deer distribution in the autumn within-home-range model, when observed use was associated with areas closer to these features than random use. However, its influence was small and varied among deer. Both the river and the canal represented a variety of resources and conditions that might be expected to prompt greater use by deer in all seasons. The most intuitive potential resource is water, but these features also represented vegetation associations (the river more so than the canal, although canals may have an associated vegetation community [Krausman et al. 1993]). But there may be reasons for deer to avoid these landscape features. In Imperial County the riparian association along the Colorado River contained an abundance of exotic vegetation (e.g., salt cedar [*Tamarix* spp.] and arundo [*Arundo donax*]) that grow in thickets. As a result these species likely make access to the river (for water) difficult, and these species have not been reported in the diets of mule deer (Marshal et al. 2004). Further, feral ass were abundant along the river (but were excluded from catchments [Andrew et al. 1997b]), and there is the potential for competition between feral ass and native ungulates (Bleich and Andrew 2000). As a consequence, deer may prefer to avoid this feature and seek forage, cover, or water in other parts of the desert, as most of our radiocollared mule deer appeared to do.

Influence of Catchments

Our work was motivated in large part by an interest in the role of catchments in the habitat management of desert mule deer in southeastern California, USA. The use of catchments to manage wildlife habitat continues to be a contentious issue in the deserts of the southwestern United States (Rosenstock et al. 1999). For decades, wildlife managers have developed water sources for desert ungulates and other wildlife under the assumption that free water is a limiting resource for these animals and that it forms an essential component of their habitat (Bleich et al. 2005). Until recently, the importance of catchments in the management of wildlife has been supported largely by observations of animals drinking from sources of free water (Rosenstock et al. 1999). Indeed, there is ample evidence that wildlife use catchments (Hervert and Krausman 1986, Hazam and Krausman 1988, Bleich et al. 1997, Boroski and Mossman 1998), and many believe the evidence is sufficient to conclude that catchments are beneficial to many desert wildlife species. More recently, however, some have begun to criticize the use of water developments, arguing that there has been little effort to determine the influences of water

sources, either on the target species or on ecosystems in general (Broyles 1995, Krausman and Czech 1998, Rosenstock et al. 1999). During the last decade, researchers have begun to use landscape-level manipulative experiments to evaluate the importance of water developments (Krausman and Etchberger 1995), yet more research is needed because of ambiguous and conflicting outcomes.

Our results provide little additional insight about the importance of catchments as a wildlife management tool. In spring, when water was most limited in the environment, existing water developments influenced observed use for some deer. However, its effect was small relative to that of slope, elevation, and NDVI rate. There is abundant evidence from other parts of the Sonoran Desert that deer use catchments for at least part of the year. In the Picacho Mountains, Arizona, USA, distance of radiocollared mule deer females to known water sources varied with season, such that they were closer than random locations during the hot season (Ordway and Krausman 1986). Similarly, Hervert and Krausman (1986) reported high seasonal water use among female deer, and strong evidence that locations of permanent water sources seasonally influenced distribution of deer. They documented nightly visits by females. When catchments known to be used by collared deer were closed, those animals moved outside of their established home ranges to find water before returning to their usual ranges (Hervert and Krausman 1986).

We considered the possibility that locations of catchments had a minor influence in the within-home-range analysis because entire home ranges were established according to locations of water; thus, the within-study-area analysis would have demonstrated whether distance to water affected home-range establishment. There was, however, little evidence for this effect (Table 7). Distance to catchments played a minor role in distinguishing observed from random home ranges in autumn. A similar result occurred for distance to river or canal; this factor had little influence in the within-home-range models in all seasons.

Although the telemetry data presented here do not support a strong effect of catchments on deer distribution, Marshal et al. (2006) used remote photography concurrently with the present study to document catchment use by radiocollared deer and the absence of use of nearby, recently built catchments. It was clear from the remote photography that deer heavily used the catchments in the study area for at least part of the year, but heavy use was not evident from the telemetry data. A reason for the disparity may have been the time of day (0700–1100 hours) and frequency of the weekly flights when compared to the 24-hour schedule on which photographic stations operated. Telemetry flights occurred after sunrise each day when deer were less likely to visit catchments, and weekly flights resulted in a smaller sample of locations per deer, making the detection of use more difficult. Hervert and Krausman (1986) reported that nearly all visits to catchments in the Picacho and Belmont Mountains, Arizona, USA, occurred after sunset and before sunrise. Deer remained inactive and removed from catchments during the day to reduce water loss and conserve energy.

The disparity between telemetry and remote photography data also may have been the result of the accuracy with which we were able to locate radiocollared animals. The resolution of the GIS

analysis was determined by size of the buffers we used around observed and random locations (i.e., 500 m). At that level of precision, however, it was impossible to know if a particular radiocollared deer was at a water development. With remote photography data, Marshal et al. (2006) could verify that collared deer were using water developments but were not able to identify individuals.

Influence of added catchments.—As mentioned earlier, new catchments were added to the periphery of the study area. This occurred during the third year of our 5-year study. These added catchments likely did not influence the outcome of this investigation, despite their proximity to the home ranges of some of our study animals. Indeed, remote photography at these new catchments demonstrated the absence of use by deer during the remainder of the study. Because radiocollared deer already had access to water sources, it was unlikely that adult females with established home ranges containing adequate water and other resources would leave those home ranges to move into unfamiliar areas merely because they contained a new source of water. Younger animals (i.e., those without established home ranges, such as emigrating yearlings) may more likely be affected by the provision of new water developments. Evaluating this possibility, however, would require collaring and monitoring deer <1 year of age, potentially for an extended period of time.

Future research into the influence of catchments on desert ungulates should consider closing catchments known to be used by radiomarked animals. The manipulation conducted by Hervert and Krausman (1986) provided a clear indication that for those deer, water was an important component of their habitats. Using a closure experiment, while simultaneously monitoring use of other important niche parameters, would progress our understanding of the relative importance of water sources and other habitat components. Further, use of GPS telemetry collars would provide locations with a precision far greater than that of this study, and during times outside of diurnal hours, for example, when deer are more likely to visit catchments (Hervert and Krausman 1986).

Management Implications

Landscape-level manipulations should continue to be a central part of evaluating the role of catchments relative to other resources in wildlife habitat management. Manipulations of the sort conducted by Hervert and Krausman (1986) would greatly facilitate our understanding of wildlife–habitat interactions where water developments are involved. Unfortunately, however, when the interest in water developments among resource agencies and hunters is taken into consideration, such a manipulation is likely to be politically difficult because of preconceived potential impacts to deer populations.

Water is only one aspect of mule deer habitat in the Sonoran Desert. Sources of forage and cover clearly are important factors in wildlife habitat. Water in the absence of forage and cover likely will not create mule deer habitat, but forage and cover in the absence of water may provide deer habitat, at least seasonally. Thus, catchments might make forage resources, which would otherwise be unavailable, available year-round. Further, where deer might otherwise make seasonal movements between parts of their range with forage and parts with water, developments may reduce the need for seasonal movements, make a greater proportion of the range and its forage available to deer, reduce competition for forage in exploited range, decrease risks associated with long-distance movements (e.g., Nicholson et al. 1997, Bleich and Pierce 2001) and, thereby, increase deer abundance (Krausman and Czech 1998). In this scenario, however, it is the combination of water sources and forage that support deer populations year-round. Nonetheless, these ideas must be tested in a landscape-level, adaptive, experimental fashion.

Literature Cited

Albert, S. K., and P. R. Krausman. 1993. Desert mule deer and forage resources in southwestern Arizona. Southwestern Naturalist 38:198–205.

Andrew, N. G. 1994. Demography and habitat use by desert-dwelling mountain sheep in the East Chocolate Mountains, Imperial County, California. Thesis, University of Rhode Island, Kingston, USA.

Andrew, N. G., V. C. Bleich, and P. V. August. 1999. Habitat selection by mountain sheep in the Sonoran Desert: implications for conservation in the United States and Mexico. California Wildlife Conservation Bulletin 12.

Andrew, N. G., V. C. Bleich, P. V. August, and S. G. Torres. 1997a. Demography of mountain sheep in the East Chocolate Mountains, Imperial County, California. California Fish and Game 83:68–77.

Andrew, N. G., L. M. Lesicka, and V. C. Bleich. 1997b. An improved fence design to protect water sources for native ungulates. Wildlife Society Bulletin 25:823–825.

Animal Care and Use Committee. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79:1416–1431.

Barten, N. L., R. T. Bowyer, and K. J. Jenkins. 2001. Habitat use by female caribou: tradeoffs associated with parturition. Journal of Wildlife Management 65:77–92.

Bergerud, A. T., and R. E. Page. 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. Canadian Journal of Zoology 65:1597–1606.

Bleich, V. C. 1999. Mountain sheep and coyotes: patterns of predator evasion in a mountain ungulate. Journal of Mammalogy 80:283–289.

Bleich, V. C., and N. G. Andrew. 2000. Mountain sheep, mule deer, and burros in the brush: flourishing wild burros impact habitat and native big game. Track 17:10–12.

Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs 134.

Bleich, V. C., C. S. Y. Chun, R. W. Anthes, T. E. Evans, and J. K. Fischer. 2001. Visibility bias and development of a sightability model for tule elk. Alces 37:315–327.

Bleich, V. C., J. G. Kie, E. R. Loft, T. R. Stephenson, M. W. Oehler, Sr., and A. L. Medina. 2005. Managing rangelands for wildlife. Pages 873–897 in C. E. Braun, editor. The wildlife techniques manual. The Wildlife Society, Bethesda, Maryland, USA.

Bleich, V. C., and B. M. Pierce. 2001. Accidental mass mortality of migrating mule deer. Western North American Naturalist 61:124–125.

Bleich, V. C., B. M. Pierce, J. Jones, and R. T. Bowyer. 2006. Variance in survival rates of young mule deer in the eastern Sierra Nevada, California. California Fish and Game 92:24–38.

Blong, B. 1993. Use of habitat by Colorado Desert deer. California Department and Fish and Game Report, Sacramento, USA.

Boroski, B. B., and A. S. Mossman. 1998. Water use patterns of mule deer (Odocoileus hemionus) and the effects of human disturbance. Journal of Arid Environments 38:561–569.

Boyce, M. S., and J. S. Waller. 2003. Grizzly bears for the Bitterroot: predicting potential abundance and distribution. Wildlife Society Bulletin 31:670–683.

Broyles, B. 1995. Desert wildlife water developments: questioning use in the southwest. Wildlife Society Bulletin 23:663–675.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Fox, K. B., and P. R. Krausman. 1994. Fawning habitat of desert mule deer. Southwestern Naturalist 39:269–275.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Griffith, B., D. C. Douglas, N. E. Walsh, D. D. Young, T. R. McCabe, D. E. Russell, R. G. White, R. D. Cameron, and K. R. Whitten. 2002. The Porcupine caribou herd. Pages 8–37 in D. C. Douglas, P. E. Reynolds, and E. B. Rhode, editors. Arctic Refuge Coastal Plain Terrestrial Wildlife Research Summaries. United States Geological Survey, Biological Resources Division, Biological Sciences Report 2002-0001, Reston, Virginia, USA.

Hazam, J. E., and P. R. Krausman. 1988. Measuring water consumption of desert mule deer. Journal of Wildlife Management 52:528–534.

Hervert, J. J., and P. R. Krausman. 1986. Desert mule deer use of water developments in Arizona. Journal of Wildlife Management 50:670–676.

Hobbs, N. T., and T. A. Hanley. 1990. Habitat evaluation: do use/availability data reflect carrying capacity? Journal of Wildlife Management 54:515–522.

Jessup, D. A., W. E. Clark, and M. A. Fowler. 1986. Wildlife restraint handbook. Third Edition. California Department of Fish and Game, Rancho Cordova, USA.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Katnik, D. D., and R. B. Wielgus. 2005. Landscape proportions versus Monte Carlo simulated home ranges for estimating habitat availability. Journal of Wildlife Management 69:20–32.

Keating, K. A., and S. Cherry. 2004. Use and interpretation of logistic regression in habitat-selection studies. Journal of Wildlife Management 68:774–789.

Krausman, P. R. 1998. The use of xeroriparian systems by desert mule deer. Arizona Riparian Council 11:11–12.

Krausman, P. R., and B. Czech. 1998. Water developments and desert ungulates. Pages 138–154 in J. M. Feller and D. S. Strouse, editors. Environmental, economic, and legal issues related to rangeland water developments. College of Law, Arizona State University, Tempe, USA.

Krausman, P. R., and R. C. Etchberger. 1995. Response of desert ungulates to a water project in Arizona. Journal of Wildlife Management 59:292–300.

Krausman, P. R., L. M. Fox, R. C. Etchberger, and K. B. Fox. 1993. Desert mule deer use of altered vegetation along the Hayden-Rhodes aqueduct, Arizona. Southwestern Naturalist 38:206–211.

Krausman, P. R., J. J. Hervert, and L. L. Ordway. 1984. Radiotracking desert mule deer and bighorn sheep with light aircraft. Pages 115–118 in P. R. Krausman and N. S. Smith, editors. Deer in the southwest: a workshop. School of Renewable Natural Resources, University of Arizona, Tucson, USA.

Krausman, P. R., J. J. Hervert, and L. L. Ordway. 1985a. Capturing deer and mountain sheep with a net-gun. Wildlife Society Bulletin 13:71–73.

Krausman, P. R., K. R. Rautenstrauch, and B. D. Leopold. 1985b. Xeroriparian systems used by desert mule deer in Texas and Arizona. Pages 144–149 in R. R. Johnson, C. D. Ziebell, D. R. Patton, P. F. Ffolliott, and R. H. Hamre, technical coordinators. Riparian ecosystems and their management: reconciling conflicting uses. United States Department of Agriculture Forest Service General Technical Report RM-120, Washington, D.C., USA.

Langvatn, R., and T. A. Hanley. 1993. Feeding-patch choice by red deer in relation to foraging efficiency. Oecologia 95:164–170.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic, Dordrecht, Netherlands.

Mares, M. A., M. R. Willig, and N. A. Bitar. 1980. Home range size in eastern chipmunks, Tamias striatus, as a function of number of captures: statistical biases of inadequate sampling. Journal of Mammalogy 61:661–669.

Marshal, J. P., V. C. Bleich, N. G. Andrew, and P. R. Krausman. 2004. Seasonal forage use by desert mule deer in southeastern California. Southwestern Naturalist 49:501–505.

Marshal, J. P., P. R. Krausman, and V. C. Bleich. 2005a. Dynamics of mule deer forage in the Sonoran Desert. Journal of Arid Environments 60:593–609.

Marshal, J. P., P. R. Krausman, and V. C. Bleich. 2005b. Rainfall, temperature, and forage dynamics affect nutritional quality of desert mule deer forage. Rangeland Ecology & Management 58:360–365.

Marshal, J. P., L. M. Lesicka, V. C. Bleich, P. R. Krausman, G. P. Mulcahy, and N. G. Andrew. 2006. Demography of desert mule deer in southeastern California. California Fish and Game 92:55–66.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223–249.

Morrison, M. L. 2001. A proposed research emphasis to overcome the limits of wildlife–habitat relationship studies. Journal of Wildlife Management 65:613–623.

Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78:483–504.

Ordway, L. L., and P. R. Krausman. 1986. Habitat use by desert mule deer. Journal of Wildlife Management 50:677–683.

Parker, K. L. 2003. Advances in the nutritional ecology of cervids at different scales. Écoscience 10:395–411.

Rautenstrauch, K. J., P. R. Krausman, F. M. Whiting, and W. H. Brown. 1988. Nutritional quality of desert mule deer forage in King Valley, Arizona. Desert Plants 8:172–174.

Riley, S. J., and A. R. Dood. 1984. Summer movements, home range, habitat use, and behavior of mule deer fawns. Journal of Wildlife Management 48:1302–1310.

Rosenstock, S. S., W. B. Ballard, and J. C. deVos, Jr. 1999. Viewpoint: benefits of wildlife water developments. Journal of Range Management 52:302–311.

Scarbrough, D. L., and P. R. Krausman. 1988. Sexual segregation by desert mule deer. Southwestern Naturalist 33:157–165.

Stewart, K. M., T. E. Fulbright, and D. L. Drawe. 2000. White-tailed deer use of clearings relative to forage availability. Journal of Wildlife Management 64:733–741.

Thompson, J. R., and V. C. Bleich. 1993. A comparison of mule deer survey techniques in the Sonoran Desert of California. California Fish and Game 79:70–75.

Tucker, C. J., and P. J. Sellars. 1986. Satellite remote sensing of primary productivity. International Journal of Remote Sensing 7:1395–1416.

Turner, R. M. 1994. Sonoran desert scrub. Pages 181–222 in D. E. Brown, editor. Biotic communities: southwestern United States and northwestern Mexico. University of Utah, Salt Lake City, USA.

Wallace, C. S. A. 2002. Extracting temporal and spatial information from remotely sensed data for mapping wildlife habitat. Dissertation, University of Arizona, Tucson, USA.

Wilmshurst, J. F., J. M. Fryxell, B. P. Farm, A. R. E. Sinclair, and C. P. Henschel. 1999. Spatial distribution of Serengeti wildebeest in relation to resources. Canadian Journal of Zoology 77:1223–1232.

Jason P. Marshal (photo, next page) has a B.S. from the University of Alaska Fairbanks (UAF), an M.S. from the University of Alberta, and a Ph.D.
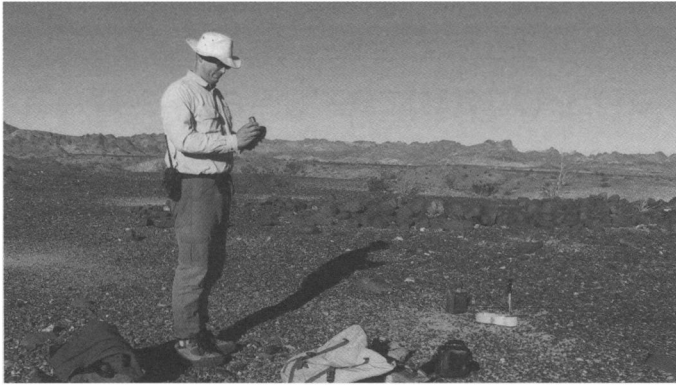
from the University of Arizona, all in the field of wildlife biology. His research interests involve population ecology, wildlife–habitat relationships, and conservation of large mammals. To continue his career only in places starting with "A," he is currently working on the ecology of introduced ungulates and their effects on native wildlife in Argentina. **Vernon C. Bleich** received B.S. and M.A. degrees from California State University, Long Beach, and a Ph.D. from UAF. He is a senior environmental scientist with the California Department of Fish and Game (CDFG), where he supervises the Sierra Nevada Bighorn Sheep Recovery Program and directs the Round Valley Project, a long-term effort examining relationships between habitat quality, prey densities, and populations of mule deer and mountain sheep in the eastern Sierra Nevada. He has been a Professional Member of the Boone and Crockett club since 1999, and in 2002 received the Outstanding Alumnus Award from the College of Science, Engineering, and Mathematics at UAF. **Paul R. Krausman** is a professor of wildlife at the University of Arizona, Tucson. He has studied desert ungulates since 1972. Paul is a certified wildlife biologist, Southwest Section representative, and editor of Wildlife Monographs. **Mickey Lynn Reed** received his B.S. in agronomy from California State University, Pomona, and his M.S. in plant physiology from the University of Arizona. He was a Peace Corps volunteer doing agricultural extension in Honduras. He currently works at the Advanced Resource Technology Group as spatial data specialist and geographic information systems project coordinator. **Nancy G. Andrew** is an Associate Wildlife Biologist with CDFG in Bermuda Dunes. Nancy received her B.A. from Fort Lewis College, an M.A. from Mankato State University, and an M.S. from the University of Rhode Island. Some of her professional interests include ecology of ungulates in arid ecosystems, and wilderness lands issues and their implications for species conservation and restoration.

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