The Southwestern Naturalist 53(3):311–318 September 2008

BODY CONDITION OF MULE DEER IN THE SONORAN DESERT IS RELATED TO RAINFALL

Jason P. Marshal,* Paul R. Krausman, and Vernon C. Bleich

School of Natural Resources, University of Arizona, Tucson, AZ 85721 (JPM, PRK)
Sierra Nevada Bighorn Sheep Recovery Program, California Department of Fish and Game, 407 West Line Street, Bishop, CA 93514 (VCB)
**Correspondent: jason.marshal@wits.ac.za*

Abstract—We investigated associations between rainfall and body condition of desert mule deer (*Odocoileus hemionus eremicus*) in the Sonoran Desert, California, using two indices of condition based on body fat: a categorical score based on subcutaneous fat and visibility of bones under the skin of free-ranging animals via remote photography, and percent fat in the marrow of long-bones of harvested males. There were positive correlations between rainfall and proportion of deer in good condition ($r = 0.60$, $P = 0.064$) and proportion of deer in fair condition ($r = 0.70$, $P = 0.017$). Proportion of deer in poor condition was negatively correlated with rainfall ($r = -0.72$, $P = 0.020$). There was evidence of a year effect on percent fat in the marrow of metacarpus and metatarsus bones ($P = 0.030$), such that years in which deer had lower average marrow fat coincided with years having lower rainfall. These findings demonstrate the importance of rainfall, likely operating through quantity or quality of forage, on body condition of mule deer, which have subsequent effects on demography. An understanding of these patterns will continue to be important for the conservation of ungulate populations in arid regions.

Resumen—Investigamos las asociaciones entre la precipitación y la condición corporal del venado bura del desierto (*Odocoileus hemionus eremicus*), en el desierto Sonorense en California, utilizando dos índices de condición basados en la grasa corporal: una calificación categórica basada en la grasa subcutánea y la visibilidad de los huesos debajo de la piel de animales silvestres vía fotografía remota, y el porcentaje de grasa en el tuétano de huesos largos en machos colectados. Hubo correlaciones positivas entre la precipitación y la proporción de venados en buena condición ($r = 0.60$, $P = 0.064$) y de los de condición intermedia ($r = 0.70$, $P = 0.017$). La proporción de los venados en mala condición se correlacionó negativamente con la precipitación ($r = -0.72$, $P = 0.020$). Se evidenció un efecto del año en el porcentaje de grasa en el tuétano de los metacarpos y metatarsos ($P = 0.030$); los años en que el promedio de la grasa del tuétano fue más bajo correspondieron con los años de menor precipitación. Éstos resultados demuestran la importancia de la precipitación, probablemente afectando la abundancia y la calidad del forraje, en la condición corporal del venado bura, lo que podría tener efectos a nivel demográfico. El conocimiento de estas relaciones contribuiría a la conservación de las poblaciones de los ungulados de las regiones áridas.

An understanding of the body condition of individuals in a wildlife population is essential for management (Cook et al., 2004*a*). Physiological health of an animal directly influences its survival and reproduction (Hobbs, 1989; Kohlmann, 1999; Cook, 2002). When generalized over a population, body condition affects changes in population abundance and dynamics (Clutton-Brock et al., 1982), as well as options for management (Cook et al., 2004*b*). Condition of animals might indicate which factors in the environment are most likely to limit a population for which greater abundance is an objective. For example, a population of deer in poor condition might indicate that scarce forage, rather than predation or other limiting factors, probably are maintaining a low population density (Ballard et al., 2001; Bowyer et al., 2005).

To evaluate body condition, wildlife managers have developed numerous indices that can be measured conveniently, but that vary with overall condition of the animal (Servello et al., 2005). Differing fat stores are used at various rates in mammals, such that any one index of condition frequently varies nonlinearly with overall body condition (Stephenson et al., 1998, 2002; Cook et al., 2001). For example, subcutaneous measures of body condition (such as thickness of back fat) change continuously with decreasing condition, up to the point where an animal becomes severely malnourished and tends to have no detectable back fat (Stephenson et al., 1998, 2002; Cook et al., 2001; Milner et al., 2003). Visceral measures of condition (e.g., kidney fat) show slow initial but rapid subsequent rates of use with a decline in condition (Cook et al., 2001). As condition continues to worsen, and subcutaneous and visceral stores of fat are exhausted, an animal switches to marrow fat as a source of energy, which is the last source of fat mobilized during severe nutritional stress (Ransom, 1965; Anderson et al., 1990). Thus, efforts to understand changes in body condition in response to varying forage resources require use of indices that span more than one phase of fat mobilization (Cook et al., 2001).

Fat stores are influenced by nutritional status, which in turn is affected by availability of forage and nutritional quality. Per capita availability of forage is influenced by interspecific competition related to population density (intrinsic variation) and by environmental influences (extrinsic variation; Choquenot, 1998). For mule deer (*Odocoileus hemionus eremicus*) in the Sonoran Desert, an environment that has high variation in rainfall and availability and quality of forage (Marshal et al., 2005*a*, 2005*b*), there is evidence that intrinsic and extrinsic factors influence population dynamics (Marshal et al., 2002). If dynamics of populations of mule deer are responses to characteristics of forage and resultant physiological mechanisms, evidence for an effect of resource limitation should be apparent in indices of body condition. Our goal was to look for evidence of these effects in mule deer of the Sonoran Desert using two measures of body condition; we visually determined condition classes of free-ranging animals using remote photography and analyzed marrow fat from long bones of harvested animals.

Materials and Methods—*Study Area*—We collected data in the California Department of Fish and Game D-12 deer-hunting zone (21,591 km), which included parts of Imperial, Riverside, and San Bernardino counties, California. This region is in the arid Lower Colorado River subdivision of the Sonoran Desert (Turner, 1994), having high temperatures (>45°C in summer), low average precipitation (ca. 70 mm/year), and high interannual variability in rainfall (range since 1914, 4–216 mm; Imperial Irrigation District, Imperial, California, in litt.). Seasons in this region were based on temperature and rainfall, with winter (cool rainy) occurring January–March, spring (hot dry) occurring April–June, summer (hot rainy) occurring July–September, and autumn (cool dry) occurring October–December. Hunting season for mule deer occurred in October–November each year.

Plant biomass in the region generally is low but varies greatly both temporally and spatially (Andrew, 1994; Marshal et al., 2005*a*). In mountainous areas, burro weed (*Ambrosia dumosa*), creosotebush (*Larrea tridentata*), brittle bush (*Encelia farinosa*), and ocotillo (*Fouquieria splendens*) were dominant species of shrubs. In riparian areas near the Colorado River, arrowweed (*Pluchea sericea*), cattails (*Typha domingensis*), and saltcedar (*Tamarix*) were common. Away from the river, >90% of plant biomass occurred in xeroriparian associations along dry desert washes (Marshal et al., 2005*a*), in which palo verde (*Parkinsonia florida*), desert ironwood (*Olneya tesota*), catclaw (*Acacia greggii*), and honey mesquite (*Prosopis glandulosa*) were common (Andrew, 1994). Mule deer in the study area occur at low densities (Thompson and Bleich, 1993), and they fluctuated between 0.05 and 0.13 deer/km^2 during data collection (Marshal et al., 2006). Other local herbivores >1 kg were bighorn sheep (*Ovis canadensis*), feral ass (*Equus asinus*), black-tailed jackrabbit (*Lepus californicus*), desert cottontail (*Sylvilagus audubonii*), and desert tortoise (*Gopherus agassizii*).

Data Collection—We used photographs taken by remote camera at wildlife water catchments during 1994, 1995, and 1997–2004 to evaluate condition of free-ranging deer. Mule deer visited catchments frequently during the hot-dry season (Marshal et al., 2006). For several weeks during this period, we used automatic film cameras attached to infrared remote triggers (TrailMaster 1500, Goodson and Associates, Inc., Lenexa, Kansas) to photograph visiting deer. Infrared emitters and receivers were placed on either side of the access point of a catchment. Cameras were placed to one side of the catchment ca. 3 m away. We adjusted sensitivity of infrared units so that only larger objects would trigger a photograph, and we set the units to take photographs >20 min apart. We conducted photographic sampling at ca. 25 catchments distributed throughout the study area. The exact number of catchments and length of sampling depended upon timing and rates of visits by deer each year. Sampling began when deer started using catchments frequently (generally late May), which was influenced by forage and rainfall the previous winter (Marshal et al., 2006). Sampling continued until summer rains began and deer moved away from catchments (July or August; Marshal et al., 2006).

We used condition classes defined by Riney (1982), which scores animals as belonging to one of three categories; good, fair, and poor (Fig. 1). Deer in good condition had a rounded rump with no visible outlines of bones on the torso. Animals in fair condition exhibited an angular rump, but outlines of bones of the torso remained obscured. Among animals in poor condition, outlines of the ribs, vertebrae, or hips were clearly visible. For each photograph, we scored condition of mule deer as good, fair, poor, or undetermined, where undetermined meant that we could not see the body clearly (e.g., it was hidden behind another animal or was partially outside the field of view). In subsequent analyses, we included only animals for which condition could be determined. We made no attempt to identify individuals in the photographs; thus, individuals were likely scored more than once, both within and among years.

Collection of long bones occurred during 2000–2003; hunters donated an entire metacarpus or metatarsus from harvested deer. We placed bones in air-tight bags and froze them immediately to prevent dehydration of the marrow. To process marrow, we defrosted the bones, cut each bone into thirds, and used the marrow from the middle one-third in our analysis. We measured hydrated mass of marrow to the nearest 0.05 g using an electronic scale (Ohaus C151, Florham Park, New Jersey) and then dried the marrow at 70°C to a constant mass (Neiland, 1970). We then reweighed dried samples and calculated the proportion of fat in the marrow sample by the dry mass divided by the wet mass.

Statistical Analysis—We used Pearson's correlation coefficient to estimate strength of the linear association between rainfall and proportion of animals in each condition class as determined from the photographs. We investigated influences of differing amounts of rainfall on the correlation coefficient, ranging from that during the month immediately prior to sampling to that accumulated during the 26 months prior to sampling. We analyzed influence of rainfall separately for proportions of animals in good, fair, and poor condition. Prior to analysis, we transformed proportions using the log of the odds to meet assumptions of linearity and homogeneity of variances in proportion data (Ramsey and Schafer, 2002).

Because only 4 years of marrow data were available, we were unable to evaluate statistically the influence of rainfall on level of marrow fat. We used single-factor analysis of variance to estimate differences in proportion of marrow fat among years. Again, we used the log-odds transformation for proportions data. Reported average proportions were back-transformed means by year and 95% confidence intervals (*CI*). We conducted a further analysis, categorizing 2000 and 2002 as dry years (23 and 11 mm annual precipitation, respectively), 2001 and 2003 as wet years (43 and 71 mm annual precipitation, respectively), marrow fat <0.90 as low, and marrow fat >0.90 as high. Then, we assigned each sample to a year category and a marrow-fat category, forming a two-by-two contingency table. We calculated the odds ratio to estimate how the odds of a high-fat sample changed between years with low and high rainfall (Ramsey and Schafer, 2002). We conducted all statistical analyses in R (R Development Core Team, 2005).

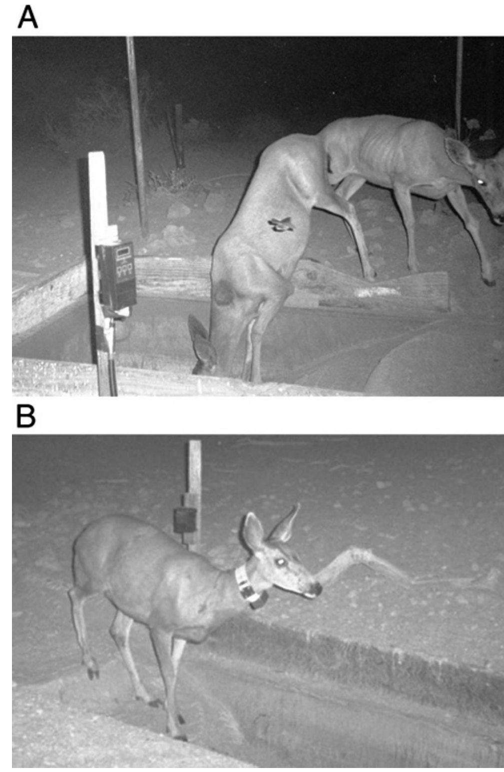

Fig. 1—Examples of mule deer (*Odocoileus hemionus*) exhibiting poor (A, right), fair (A, left), and good (B) condition in photographs taken remotely at wildlife water developments, Sonoran Desert, southeastern California, 1994–2004.

Results—*Condition*—We classified condition from 9,548 observations of deer over 10 years of photographic sampling (Table 1). Proportion of deer in good condition ranged from <0.01 in 2 dry years (1997 and 2000) to 0.44 (95% *CI*, 0.38–0.51) in 1998. Proportion of animals in fair condition ranged from 0.85 (95% *CI*, 0.73–0.97) in 1994 to 0.18 (95% *CI*, 0.17–0.20) in 2000. Proportion of animals in poor condition ranged from 0.06 (95% *CI*, 0.05–0.07) in 2004 to 0.82 (95% *CI*, 0.80–0.83) in 2000.

Correlation coefficients for each condition class varied according to amount of accumulated rainfall with which it was correlated (Fig. 2). Correlation between log-odds transformed proportion of animals in good condition and accumulated rainfall increased rapidly from 1 to 4 months, reaching maximum correlation at 6 months (0.60, two-sided $P = 0.064$; Fig. 3); from there, correlation decreased slowly up to 26 months of accumulated rainfall. Correlation for animals in fair condition reached a peak in the first 3 months of accumulated rainfall, having a value of 0.70 (two-sided $P = 0.017$; Fig. 3) at month 3, and then decreasing to 14 months.

TABLE 1—Proportion of photographed mule deer (*Odocoileus hemionus*) in each condition class, determined by remote photography at wildlife water developments in the Sonoran Desert, California.

Year	Number of deer	Proportion in good condition	Proportion in fair condition	Proportion in poor condition	Precipitation (mm)
1994	34	0.06	0.85	0.09	71
1995	48	0.31	0.58	0.10	82
1996	0				
1997	305	<0.01	0.41	0.59	31
1998	230	0.44	0.44	0.12	127
1999	446	0.10	0.46	0.44	52
2000	2,155	<0.01	0.18	0.82	39
2001	512	0.17	0.46	0.36	59
2002	3,117	0.27	0.57	0.17	0
2003	1,329	0.36	0.55	0.09	56
2004	1,372	0.17	0.32	0.51	90

From there, correlation rose to 0.69 (two-sided $P = 0.028$) at 20 months. The relationship between correlation coefficient and accumulated rainfall among deer in poor condition was a mirror image of that for deer in good condition. Negative correlation reached a maximum at 7 months (-0.72, two-sided $P = 0.020$; Fig. 3).

Given the correlation between proportion of deer in each condition class and accumulated rainfall the previous 6–7 months, we conducted an additional exploratory analysis to investigate the potential to predict condition of mule deer from rainfall. Animals in poor condition were easiest to distinguish in photographs, because the outlines of bones beneath the skin were highly noticeable. Thus, we used the reciprocal of proportion of animals in poor condition (i.e., proportion of deer in good and fair condition combined) as the response variable in a regression analysis to evaluate effects of rainfall the previous 7 months (accumulated rainfall) and population density. Density was based on an index of abundance to look for possible density-dependent effects on condition; these data came from the same remote-photography fieldwork used for the present analysis (number of deer observed in photographs/catchment-day; Marshal et al., 2006). Regression analysis revealed positive effects of both accumulated rainfall and index of abundance on log-odds-transformed proportion of deer in good and fair condition combined ($-2.96 + 0.05$ [accumulated rainfall] $+ 0.20$ [index of abundance]; $F_{2,5} = 14.25$, $P = 0.008$, $r = 0.85$). We further explored the possibility that these data could be used to predict abundance of deer from rainfall and body condition; thus, we rearranged the variables and refitted the model. The resulting linear model was: index of abundance = 14.13 − 0.21 (accumulated rainfall) + 3.59 (log-odds-transformed proportion of deer in good and fair condition combined) ($F_{2,5} = 8.90$, $P = 0.022$, $r^2 = 0.78$). This fit of the model was not as close as that for the previous configuration of variables, but it does suggest a method by which remote-photography data and information on rainfall and body condition of mule deer might be used to predict abundance.

Marrow Fat—We collected 58 metacarpi and 8 metatarsi. There was no evidence of a difference in percent marrow fat between type of bone ($P = 0.356$); thus, we combined all bones for analysis. There was evidence for an effect of year on proportion of marrow fat $F_{3,62} = 3.19$, $P = 0.030$), with higher average marrow fat coinciding with those years having higher annual rainfall (Fig. 4). Average proportion of marrow fat ranged from 0.82 (95% *CI*, 0.70–0.90) in 2000 to 0.95 (95% *CI*, 0.92–0.97) in 2003 (Fig. 4). Of the samples, 54% ($n = 13$) and 43% ($n = 14$) had low marrow fat during the 2 dry years, whereas 12% ($n = 17$) and 9% ($n = 22$) had low marrow fat for the 2 wet years. We estimated the odds of a sample of long bone having marrow fat <0.90 during a dry year to be 8.1 times the odds of having low marrow fat during a wet year (95% *CI*, 2.3–29.2).

DISCUSSION—Body condition of mule deer in the Sonoran Desert of California was related to rainfall patterns. Ideally, an understanding of the mechanisms that link environment and condition of mule deer should occur directly

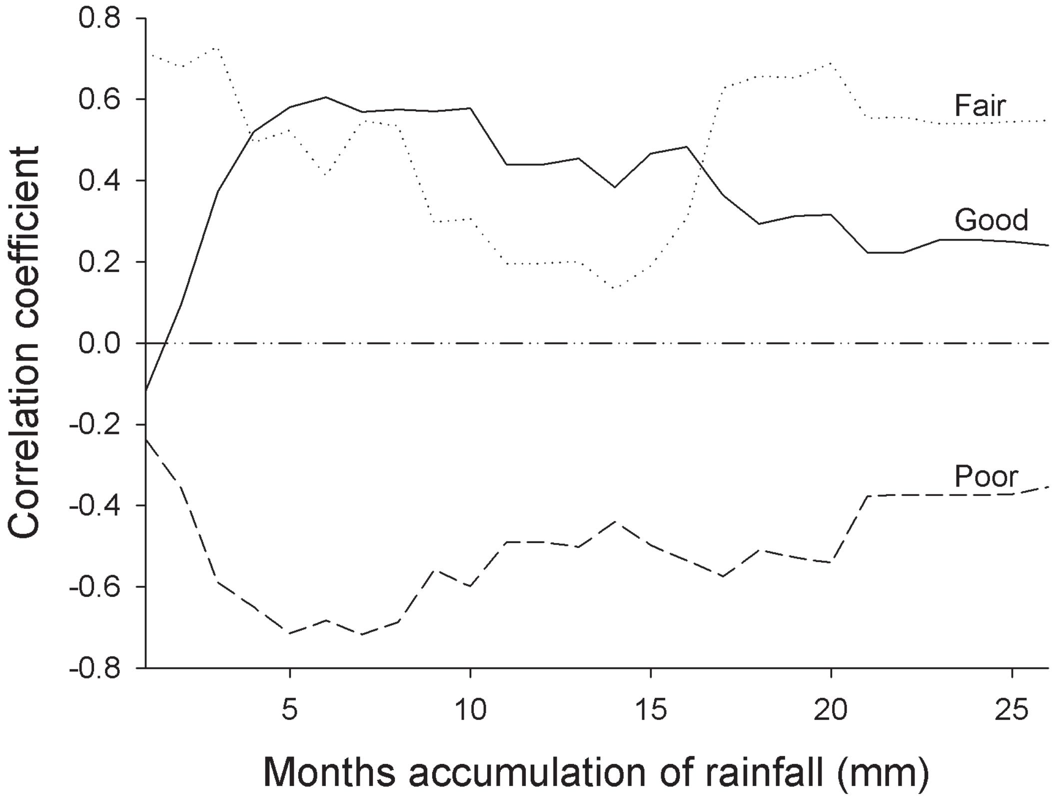

Fig. 2—Effect of differing accumulation of rainfall before each annual photographic-sampling period on correlation against log-odds-transformed proportions of mule deer (*Odocoileus hemionus*) exhibiting good, fair, and poor condition, Sonoran Desert, southeastern California, 1994–2004.

via characteristics of plants and forage. However, rainfall was a useful index that was easier to measure and has been shown to be related to biomass and nutritional quality of forage in our study area (Marshal et al., 2005*a*, 2005*b*).

The strongest correlations involving proportions of mule deer in good and poor condition were related to 6–7 months of accumulated rainfall; however, high correlations continued out to 8–12 months before sampling. Thus, rainfall that most affected condition of mule deer at the time of photographic sampling fell after the previous autumn and winter, but there is some suggestion that body condition during any particular sampling period was influenced by rainfall and forage patterns stretching back to the previous year. The link between a rainfall event and body condition includes several steps that result in a lag between precipitation and its influence on wildlife populations. In arid regions, vegetation responds rapidly to rainfall events of sufficient magnitude (Beatley, 1974), with forage increasing in biomass and nutritional quality (Marshal et al., 2005*a*, 2005*b*). After rainfall events and during prolonged dry periods, forage dies back and becomes poorer in nutritional quality (Marshal et al., 2005*b*). The rate at which this occurs is a function of the intensity and timing of rainfall and the duration of rainy seasons (Noy-Meir, 1973), but in our study area these processes generally occur on a time-scale of months. A winter with above-average rainfall might permit a relatively high abundance of forage resources to persist into spring (hot-dry season), sustaining mule deer until monsoon rains occur in summer. During winters with below-average rainfall, forage might remain scarce through the hot-dry season until summer rains. Thus, the condition of mule deer observed in photographs taken in May and June likely is affected primarily by precipitation that fell since the previous winter, 6–7 months earlier.

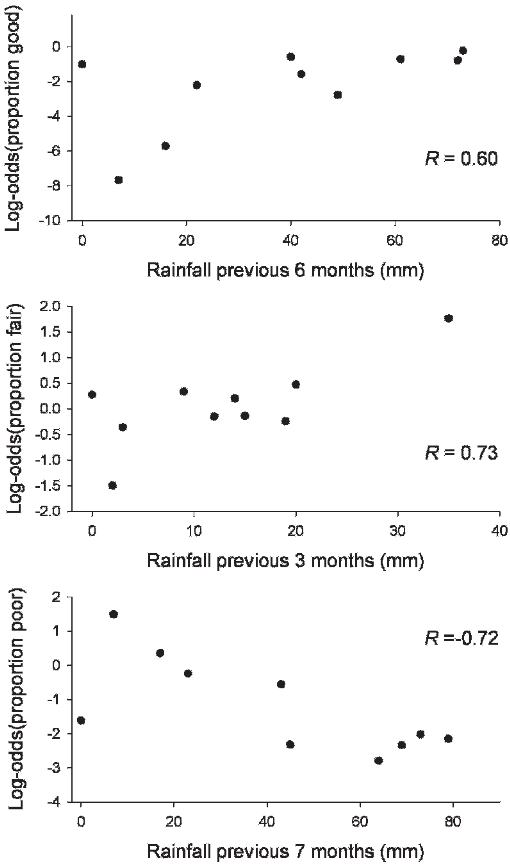

FIG. 3—Scatter plots for log-odds-transformed proportions of mule deer (*Odocoileus hemionus*) exhibiting good, fair, and poor condition against the accumulation of rainfall that produced the highest correlation coefficient, Sonoran Desert, southeastern California, 1994–2004.

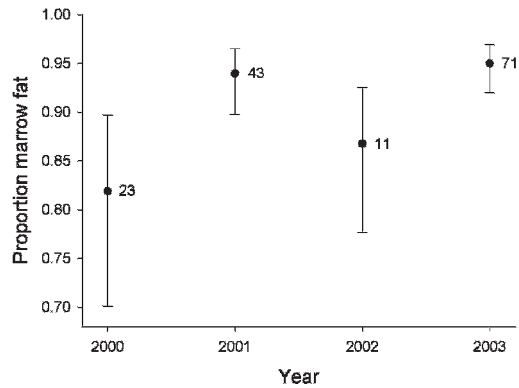

FIG. 4—Back-transformed means and 95% confidence intervals for proportion of fat in long-bone marrow collected from harvested mule deer (*Odocoileus hemionus*), Sonoran Desert, southeastern California, 2000–2003. Numbers next to each mean are the 12 months of accumulated rainfall for each year ending the month before each hunting season.

The high initial correlation for proportion of mule deer in fair condition suggests that there is a separate influence of rainfall that occurs during late winter (March–April) and affects the proportion of animals in fair condition. The additional peak that occurred at 17–20 months suggests a lingering influence of forage conditions from the previous year, and provides evidence of the importance of winter rainfall, not just for sustaining deer through a period of scarcity of forage to the next rainy season, but for influencing the condition of adult females during a time immediately before onset of parturition (July–October). Support for the longer-term effects of forage conditions on subcutaneous stores of fat also has been reported for moose (*Alces alces*; Stephenson et al., 1998), elk (*Cervus elaphus*; Cook et al., 2001), and reindeer (*Rangifer tarandus*; Milner et al., 2003).

Condition classes developed by Riney (1982) were based on deposition of subcutaneous fat and, as indicated by our analyses, could be influenced by rainfall and forage conditions over the previous 20 months. Subcutaneous fat is mobilized during earlier phases of prolonged scarcity of forage (Stephenson et al., 1998; Cook et al., 2001). Marrow fat, however, is one of the last sources of fat that is mobilized during scarcity of forage (Ransom, 1965; Anderson et al., 1990). When an ungulate begins to mobilize marrow fat, that animal has reached a state of severe nutritional stress (Fuller et al., 1986; Husseman et al., 2003). Thus, a deviation from a fat percentage near 100% is an indication that an animal has exhausted all other energy stores (Holand, 1992; Cook et al., 2001). Based on a threshold of 90% marrow fat, we discovered that during the 2 dry years, a substantially higher proportion of deer that we sampled indicated severe nutritional stress than during the 2 wet years. Indeed, deer killed by automobiles in our study area exhibited little subcutaneous or visceral fat during dry periods (J. P. Marshal et al., in litt.). In an environment characterized by high variability in rainfall and forage, periods of scarcity of forage severe enough to cause substantial nutritional stress in mule deer probably are common.

If density dependence in condition were operating, the index of abundance and proportion of deer in good and fair condition combined would have had a negative relationship. That they were positively related indicates that body condition and abundance were related positively to rainfall; perhaps, suggesting that condition was affected primarily by extrinsic (i.e., density-independent) sources of variation in availability of forage (Keyser et al., 2005). Evaluation of body condition is a common method of judging density of a wildlife population with respect to carrying capacity (Skogland, 1983; Choquenot, 1991). According to the typical model of density dependence, as a population tends toward carrying capacity, intraspecific competition for forage increases as per capita availability of forage decreases. Lower forage per capita means less, or poorer-quality, forage available to individuals, a pattern reflected in the decline in body condition of individuals as the population increases. Thus, measuring condition is a means of evaluating the relationship between a population and its forage resources (i.e., the status of a population in relation to carrying capacity). This relationship depends, however, on the assumption that carrying capacity is somewhat constant (Caughley, 1976). In the Sonoran Desert of southeastern California, there is evidence that carrying capacity varies markedly from year to year (Marshal et al., 2002, 2005*a*). Evidence presented here supports this finding; that is, there was no detected association between abundance and proportion of animals in good and fair condition in the population, but there was evidence for a relationship with rainfall (an index of availability of forage). Continuing research into deer-resource interactions in deserts, and their resultant effects on body condition and demography, will need to consider the variable nature of forage resources and carrying capacity. Direct measurement of resources and factors that influence them will contribute greatly to our understanding of population dynamics of mule deer and to its application to long-term conservation of desert ungulates.

Comments of two anonymous reviewers contributed greatly to production of this paper. This research was a cooperative effort between California Department of Fish and Game, Desert Wildlife Unlimited, Imperial County Fish and Game Commission, and the University of Arizona School of Natural Resources. We are grateful to the hunters who contributed long-bones from harvested mule deer. We thank wardens J. Brana, R. McBride, C. Sassie, B. Straatmann, T. Stepson, and G. Verbrugge of the California Department of Fish and Game for assistance with collection of samples, and N. Andrew, L. Lesicka, G. Mulcahy, and J. Wehler for assistance with collection of samples, remote photography, and other logistical support. E. Salgado assisted with analysis of photographs and L. Schnepp assisted with laboratory analysis of long-bone marrow. C. Trochine assisted with translation of the abstract. Funding was provided by the Rob and Bessie Welder Wildlife Foundation, California Department of Fish and Game, Desert Wildlife Unlimited, Imperial County Fish and Game Commission, and the University of Arizona School of Natural Resources. This is a contribution from the Deer Herd Management Plan Implementation Program of the California Department of Fish and Game, and is contribution 667 of the Rob and Bessie Welder Wildlife Foundation and professional paper 57 from the Eastern Sierra Center for Applied Population Ecology.

Literature Cited

Anderson, A. E., D. C. Bowden, and D. E. Medin. 1990. Indexing the annual fat cycle in a mule deer population. Journal of Wildlife Management 36: 579–594.

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

Ballard, W. B., D. Lutz, T. W. Keegan, L. H. Carpenter, and J. C. De Vos. 2001. Deer-predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. Wildlife Society Bulletin 29:99–115.

Beatley, J. C. 1974. Pheonological events and their environmental triggers in Mojave Desert ecosystems. Ecology 55:856–863.

Bowyer, R. T., D. K. Person, and B. M. Pierce. 2005. Detecting top-down versus bottom-up regulation of ungulates by large carnivores: implications for conservation of biodiversity. Pages 342–361 in Large carnivores and the conservation of biodiversity (J. C. Ray, K. H. Redford, R. S. Steneck, and J. Berger, editors). Island Press, Washington, D.C.

Caughley, G. 1976. Wildlife management and the dynamics of ungulate populations. Pages 183–246 in Applied biology (T. H. Coaker, editor). Volume 1. Academic Press, London, United Kingdom.

Choquenot, D. 1991. Density-dependent growth, body condition, and demography in feral donkeys: testing the food hypothesis. Ecology 72: 805–813.

CHOQUENOT, D. 1998. Testing the relative influence of intrinsic and extrinsic variation in food availability on feral pig populations in Australia's rangelands. Journal of Animal Ecology 67:887–907.

CLUTTON-BROCK, T. H., F. E. GUINNESS, AND S. D. ALBON. 1982. Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago, Illinois.

COOK, J. G. 2002. Nutrition and food. Pages 259–349 in North American elk: ecology and management (D. E. Toweill and J. W. Thomas, editors). Smithsonian Institution Press, Washington, D.C.

COOK, J. G., B. K. JOHNSON, R. C. COOK, R. A. RIGGS, T. DELCURTO, L. D. BRYANT, AND L. L. IRWIN. 2004*a*. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155:1–61.

COOK, R. C., J. G. COOK, AND L. D. MECH. 2004*b*. Nutritional condition of northern Yellowstone elk. Journal of Mammalogy 85:714–722.

COOK, R. C., J. G. COOK, D. L. MURRAY, P. ZAGER, B. K. JOHNSON, AND M. W. GRATSON. 2001. Development of predictive models of nutritional condition for Rocky Mountain elk. Journal of Wildlife Management 65:973–987.

FULLER, T. K., P. L. COY, AND W. J. PETERSON. 1986. Marrow fat relationships among leg bones of white-tailed deer. Wildlife Society Bulletin 14:73–75.

HOBBS, N. T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. Wildlife Monographs 101:1–39.

HOLAND, O. 1992. Fat indices versus ingesta-free body-fat in European roe deer. Journal of Wildlife Management 56:241–245.

HUSSEMAN, J. S., D. L. MURRAY, G. POWER, AND D. M. MACK. 2003. Correlation patterns of marrow fat in Rocky Mountain elk bones. Journal of Wildlife Management 67:742–746.

KEYSER, P. D., D. C. GUYNN, AND H. S. HILL. 2005. Population density–physical condition relationships in white-tailed deer. Journal of Wildlife Management 69:356–365.

KOHLMANN, S. G. 1999. Adaptive fetal sex allocation in elk: evidence and implications. Journal of Wildlife Management 63:1109–1117.

MARSHAL, J. P., P. R. KRAUSMAN, AND V. C. BLEICH. 2005*a*. 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. 2005*b*. Rainfall, temperature, and forage dynamics affect nutritional quality of desert mule deer forage. Rangeland Ecology and Management 58:360–365.

MARSHAL, J. P., P. R. KRAUSMAN, V. C. BLEICH, W. B. BALLARD, AND J. S. MCKEEVER. 2002. Rainfall, El Niño, and dynamics of mule deer in the Sonoran Desert, California. Journal of Wildlife Management 66: 1283–1289.

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.

MILNER, J. M., A. STEIN, R. J. IRVINE, S. D. ALBON, R. LANGVATN, AND E. ROPSTAD. 2003. Body condition in Svalbard reindeer and the use of blood parameters as indicators of condition and fitness. Canadian Journal of Zoology 81:1566–1578.

NEILAND, K. A. 1970. Weight of dried marrow as an indicator of fat in caribou femurs. Journal of Wildlife Management 34:904–907.

NOY-MEIR, I. 1973. Desert ecosystems: environments and producers. Annual Review of Ecology and Systematics 4:25–51.

R DEVELOPMENT CORE TEAM. 2005. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RAMSEY, F. L., AND D. W. SCHAFER. 2002. The statistical sleuth: a course in methods of data analysis. Second edition. Duxbury, Pacific Grove, California.

RANSOM, A. B. 1965. Kidney and marrow fat as indicators of white-tailed deer condition. Journal of Wildlife Management 29:397–398.

RINEY, T. 1982. Study and management of large mammals. John Wiley & Sons, New York.

SERVELLO, F. A., E. C. HELGREN, AND S. R. MCWILLIAMS. 2005. Techniques for wildlife nutrition ecology. Pages 554–590 in Techniques for wildlife investigations and management (C. E. Braun, editor). The Wildlife Society, Bethesda, Maryland.

SKOGLAND, T. 1983. The effects of density-dependent resource limitation on size of wild reindeer. Oecologia (Berlin) 60:156–168.

STEPHENSON, T. R., V. C. BLEICH, B. M. PIERCE, AND G. P. MULCAHY. 2002. Validation of mule deer body composition using in vivo and post-mortem indices of nutritional condition. Wildlife Society Bulletin 30:557–564.

STEPHENSON, T. R., K. J. HUNDERTMARK, C. C. SCHWARTZ, AND V. VAN BALLENBERGHE. 1998. Predicting body fat and body mass in moose with ultrasonography. Canadian Journal of Zoology 76:717–722.

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.

TURNER, R. M. 1994. Sonoran desertscrub. Pages 181–222 in Biotic communities: southwestern United States and northwestern Mexico (D. E. Brown, editor). University of Utah Press, Salt Lake City.

Submitted 2 November 2006. Accepted 11 December 2007. Associate Editor was Cheri A. Jones.