CALIFORNIA FISH AND GAME
California Fish and Game 95(3):128-139 2009

THERMAL LANDSCAPES AND RESOURCE SELECTION BY BLACK-TAILED DEER: IMPLICATIONS FOR LARGE HERBIVORES

R. TERRY BOWYER
Department of Biological Sciences
921 South 8th Avenue, Stop 8007
Idaho State University
Pocatello, ID 83209-8007
Email: bowyterr@isu.edu

JOHN G. KIE
Department of Biological Sciences
921 South 8th Avenue, Stop 8007
Idaho State University
Pocatello, ID 83209-8007

ABSTRACT

We studied black-tailed deer, *Odocoileus hemionus columbianus*, in northern California, USA, during winter to test the importance of thermal conditions on habitat selection. During warm days, temperatures from black-body devices were higher than ambient air temperatures in habitats other than live oak, *Quercus wislizenii*, but were closer to ambient temperatures in dense live-oak cover. Deer were more likely to occur in or near (≤ 150 m) live oak than were random locations, spending 80% of their time in or near live oak during day and 70% of their time in that habitat at night. We determined whether deer would occur in or near live oak based on the interaction between wind speed and relative humidity, which had an 18% probability of being the best model. We formulated a resource-selection function, which indicated that a point in or near live-oak cover was more likely to be a deer location than a random point (*P* = 0.004). When it was windy, habitat was not a significant predictor of deer locations versus random points (*P* > 0.05). When it was calm, not only was habitat a significant predictor (*P* = 0.035), but the model performed substantially better than did the model for all wind conditions based on Akaike Information Criterion (AIC) scores. We concluded that black-tailed deer in winter pelage were using live-oak thickets to ameliorate heat gain on calm, warm days with low humidity, but acknowledge that other factors, such as risk of predation, also may play a role. Our results have implications for assessing thermal data in studies of resource selection by other large herbivores.

INTRODUCTION

Recent studies of captive animals have resulted in a better understanding of thermal requirements of ungulates in coping with climatic stress (Parker and Robbins 1984, Renecker and Hudson 1986, Parker and Gillingham 1990, Cook et al. 1998). Traditional studies of habitat selection by large mammals, however, rarely have incorporated differences resulting from variable abiotic conditions. Recently, increasing attention has been paid to daily and seasonal cycles in habitat use (Ager et al. 2003). Moreover, use of habitats by ungulates in northern latitudes to ameliorate abiotic extremes during winter has been a concern of resource managers (Cook et al. 1998), and computer simulations have demonstrated the value of canopy cover (Porter et al. 2002). Nevertheless, when tested empirically, captive North American elk, Cervus elaphus, lost less body mass during winter when constrained to habitats with no overstory tree cover compared with areas with cover, presumably because of the benefits of additional solar radiation (Cook et al. 1998). Hence, a more thorough understanding of habitat use by ungulates requires an integration of thermal characteristics in models of resource selection. Critical questions (Parker and Gillingham 1990) are (1) to what degree, and (2) in what manner do thermoregulatory constraints influence habitat selection by large mammals?

Our purpose was to develop methods to assess the role of the thermal environment in habitat selection, and test if weather variables affected selection of habitats by black-tailed deer, O. h. columbianus, during winter. This research also should provide direction relative to the importance of including thermal data in models of habitat selection for large herbivores.

STUDY AREA

We conducted research on the Tehama Wildlife Management Area in northern California, USA (121° 50’W, 40° 15’N), approximately 30 km east-northeast of Red Bluff. The area encompassed 17,850 ha of winter range used by the East Tehama deer herd. The study site was a 3.1 km × 3.1 km area at about 600 m in elevation with little topographic relief (Fig. 1). Data were collected between 15 January and 12 March 1991. The climate was Mediterranean; winters were cool and wet and summers were hot and dry. Annual precipitation averaged 960 mm in nearby Redding, California, with most of that falling as rain between October and May.

Major habitat types were defined based on the dominant overstory tree species. Deciduous blue oak, Quercus douglasii, savanna and blue oak woodland were the most common habitat types. Most overstory tree species were blue oaks, with scattered gray pines, Pinus sabiniana, non-deciduous interior live oaks, Q. wislizenii, and California buckeyes, Aesculus californica. Wedgeleaf ceanothus, Ceanothus cuneatus, was the most common shrub in blue oak habitat types, but scrub oak, Q. berberidifolia, also was present (Kie and Boroski 1995).

An understory of annual grasses and forbs was common. Typical species included slender wild oat, Avena barbata, ripgut brome, Bromus diandrus, soft chess, B. hordeaceus, redstem filaree, Erodium cicutarium, blue dicks, Dichelostemma capitatum, and bur clover, Medicago polymorpha. Annual grasses and forbs germinated with autumn rains in October each year. During cool winter months, these annuals provided limited amounts of high-quality forage for deer. With warming weather

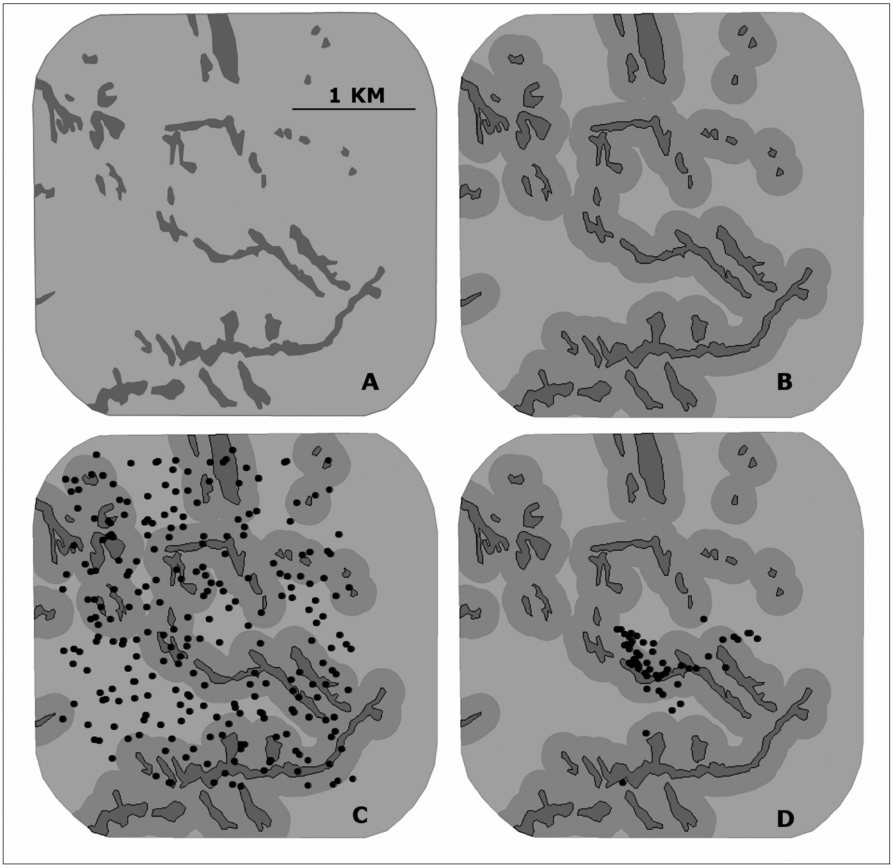

Figure 1: Study site at Tehama Wildlife Management Area, California, USA, showing: a) live-oak cover (dark gray), and other, non-cover habitats (light gray), b) live-oak cover with a 150-m buffer (medium gray), c) location of random points, and d) locations of an individual deer between 15 January and 12 March 1991. Extent of study site extent was approximately 3.1 × 3.1 km.

in February and March, growth rates of plants increased and herbaceous forage was both abundant and nutritious. As annuals began to dry and cure in April and May, forage quality declined (Kie and Boroski 1995).

Blue oak-gray pine and gray pine habitats were dominated by a mixture of those trees. Herbaceous understory was similar to that in blue oak-dominated habitats, but was generally less productive in those types with higher vertical closures of overstory canopy. Small patches of non-deciduous interior live oak occurred in narrow stringers (Fig. 1). These habitats were often dense, closed-canopy stands with little or no understory. Where stands were open, shrubs included buck brush, California coffeeberry, Rhamnus californica, mountain mahogany, Cercocarpus betuloides, western redbud, Cercis occidentalis, poison oak, Toxicodendron diversilobum, and manzanita, Arctostaphylos spp. We combined live-oak habitats with closed overstories, and more open areas into two habitat types for purposes of analysis.

METHODS

We mapped habitat types based on 1:7,850 panchromatic aerial photographs. Vegetation types on our study area occurred in discrete patches; it was relatively easy to draw boundaries between types. Moreover, recognizing only two habitat types (dense stands of live oak, and more open areas) made this process simple.

We established a weather station in open grassland on the study site that recorded data at 10-min intervals including air temperature (°C) in a shaded enclosure, relative humidity (%), solar radiation (watts * m^{-2}), wind speed (m * min^{-1}), and precipitation (mm * 10 min^{-1}). We also placed six black-body thermocouple devices at different locations; two in live-oak cover and four in other more open habitats. These devices consisted of a thermocouple placed inside a copper toilet-bowl float approximately 10 cm in diameter painted flat black. Each device was constructed with two floats placed at 0.3 m and 1 m above the ground to represent a deer lying and standing, respectively. Data from thermocouples were recorded at 10-min intervals and then averaged to encompass temperatures experienced by bedding or standing deer. Black-body temperatures are related to ambient air temperature, solar radiation, and wind speed; these devices have been used previously to represent thermal environments experienced by a variety of animals (Bakken 1992). Our black-body analogues were smaller than the body mass of a deer and hence, gained and lost heat more rapidly than an individual animal. Consequently, these devices underestimate the actual radiant heat load on a deer, thereby providing a conservative estimate of the heat load and subsequent response of deer to thermal environments.

We used a subset of data from a previously conducted, broader study on effects on cattle grazing on black-tailed deer during winter in northern California (Kie and Boroski 1995) to address whether weather variables affected selection of habitats by black-tailed deer. No cattle were present, however, in the portions of our study area during the time we collected data for this study. Adult female deer were captured between November 1989 and January 1993 with drop nets, clover traps, or by driving them into panel nets with a helicopter (Schemnitz 1994). Captured deer were fitted with VHF radio-telemetry collars (Telonics Inc., Mesa, Arizona, USA) and monitored periodically over 20-h periods with a receiver and a dual-null, direction-finding antenna array. Locations were calculated from synchronous azimuths based on null signals from two or more permanent antenna sites. We monitored locations (n = 249) for five deer between 15 January and 12 March 1991 in our analysis. Activities of deer were not sampled as part of this research; direct observations of deer in dense live-oak habitat would have been difficult. Diel activity patterns for mule deer, however, are well documented, with increases in standing and foraging during crepuscular periods (Eberhardt et al. 1984, Bowyer and Kie 2004). Our 20-h sampling periods incorporate such changes in deer activity across their diel cycle and their subsequent effects on habitat selection. All experimental protocols followed animal welfare guidelines subsequently established by the American Society of Mammalogists (American Society of Mammalogists 1998).

We placed radio-telemetry collars at 68 random points across the study site and used differential Global Positioning System (GPS) data to obtain the true location of each collar. The median error between the estimated and assumed known location was 149.7 m. Consequently, we placed a 150-m buffer around each patch of live-oak cover and classified each deer location as either being in or near live-oak cover (i.e., within the 150-m buffer) or in other habitats. For comparison, we generated a similar set of random locations (n = 249) from a uniform distribution constrained by the range of X and Y coordinates of actual locations of deer (i.e., a matched-case analysis; Boyce 2006). This procedure is equivalent to buffering locations of deer to deal with location errors, and also allowed a clear cut determination of whether a deer was in or near live-oak cover (i.e., a binomial response). Moreover, buffering locations of deer would have required determining the relative proportions of habitat in each buffer (Nicholson et al. 1997), and prevented us from using logistic regression as an analytical tool. We categorized wind conditions by inspecting data on wind speed obtained by the weather station. Calm was defined as wind speeds ≤ to the median (102 m * min^{-1}), whereas windy was > the median value.

We calculated simple correlation coefficients (r) between black-body temperatures and environmental variables measured at the onsite weather station. To determine how air temperature, relative humidity, solar radiation, wind speed, and precipitation affected locations of deer (in or near live-oak cover or in other habitats), we used both univariate and all possible subsets of logistic regression (PROC LOGISTIC—SAS Institute 1999). We examined the best 1-variable, 2-variable, 3-variable,…n-variable models including interaction terms, with individual animal forced into each model to account for potential differences among individuals. Model fits were determined based on scores for Akaike Information Criterion (AIC, Burnham and Anderson 1998).

We used conditional logistic regression (PROC PHREG—SAS Institute 1999) to formulate simple resource-selection functions distinguishing between deer locations and random points based on habitat type (in or near live-oak cover, or in other habitats). Data were stratified or blocked by individual, to make the individual rather than number of points the sampling unit, which avoided pseudoreplication, yet allowed us to use all of our samples on deer locations and random points (Boyce and McDonald 1999, Boyce 2006). As a result, we used AIC scores adjusted for small sample sizes (AIC_C—Burnham and Anderson 1998). We reasoned that if thermal conditions affected resource selection by deer, they should do so across broad vegetation types indicative of closed canopy compared with more open areas, as well as integrating effects of food and water on resource selection across these habitats.

RESULTS

Temperatures of black-body thermocouples in live-oak cover were slightly higher than ambient air temperatures during daylight hours and slightly lower than ambient during the night. Black-body temperatures in open habitats, however, were much warmer during the day and lower at night than ambient air temperatures (Fig. 2). Thermocouple temperatures for black bodies placed in live-oak cover were significantly ($P < 0.05$) correlated with air temperature ($r = 0.89$), solar radiation ($r =$

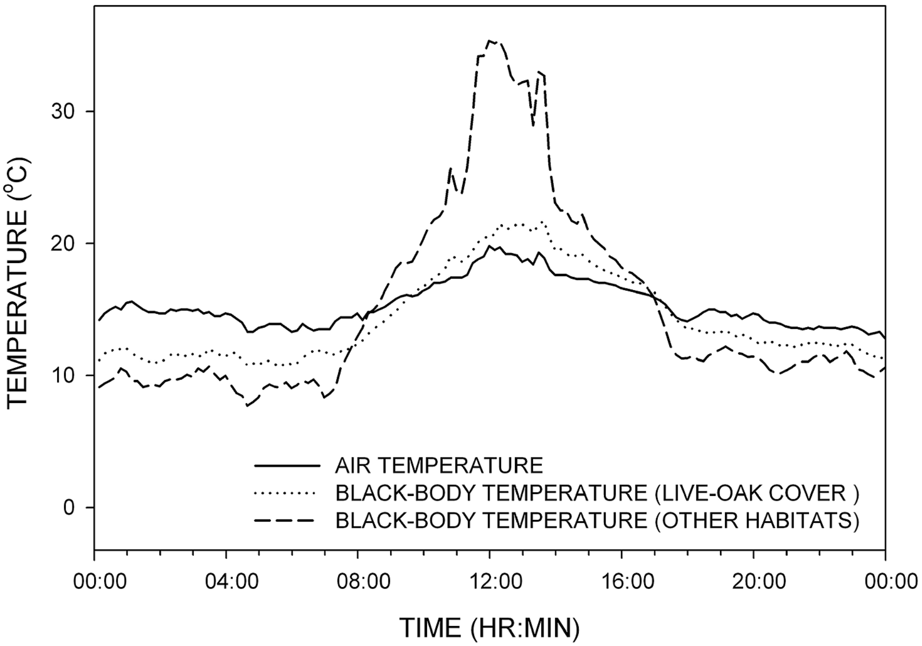

Fig. 2. Comparison of air temperature and temperatures inside black-bodies placed in live-oak cover and non-cover habitats on a representative warm day (15 February 1991) at Tehama Wildlife Management Area, California, USA. Air temperature is from the single weather station; black-body temperatures represent means from six black-body devices.

0.65), and relative humidity ($r = -0.28$). For black bodies placed in other habitats, thermocouple temperatures were significantly ($P < 0.05$) correlated with air temperature ($r = 0.73$), solar radiation ($r = 0.89$), and relative humidity ($r = -0.25$). In both habitats, thermocouple temperatures for black bodies were only weakly correlated with wind speed ($r < 0.15$).

Deer were located in or near live-oak cover 80% of the time during daylight hours and 70% of the time at night. By comparison, only 65% of random locations were in or near live-oak cover. In using logistic regression to predict whether deer occurred in or near live-oak cover or in other habitats based on air temperature, relative humidity, solar radiation, precipitation, wind speed (and interactions among wind speed with air temperature, relative humidity, and solar radiation), we determined that only wind speed ($P = 0.07$) and the interaction between wind speed and relative humidity ($P = 0.04$) were significant or nearly so. All other variables and interactions tested were not significant ($P \geq 0.10$). The most parsimonious logistic multiple-regression model used to distinguish whether deer occurred in or near live-oak cover was based on the interaction between wind speed and relative humidity, which had an 18% probability of being the best model (AIC weight, $w_i = 0.18$). Six other models, however, could not be distinguished from the best model based on the criterion ΔAIC ≤ 2 (Table 1).

Table 1. Logistic regression models distinguishing deer locations in or near live oak cover versus other habitats during winter at Tehama Wildlife Management Area, California, USA, ranked by AIC values and AIC weights (w_i). Variables were: Air (air temperature, 0^C), Rh (relative humidity, %), Solar (solar radiation, watts * m^{-2}), Wspeed (wind speed, m * min^{-1}) and Ppt (precipitation, mm * 10 min^{-1}). Individual (ID) was forced into each model to account for variability among individual animals. The first seven models are indistinguishable based on the criterion ΔAIC $\leq$ 2 and are shown here. AIC weights (w_i) were calculated based on all 22 possible models, hence, weights for these top 7 models do not sum to 1.

Model	AIC	w_i
(Rh*Wspeed) (ID)	283.139	0.180
(Wspeed) (ID)	284.274	0.131
(Air) (ID)	285.442	0.129
(Air*Wspeed) (Rh*Wspeed) (ID)	283.781	0.111
(Wspeed) (Air*Wspeed) (ID)	283.810	0.102
(Solar*Wspeed) (Rh*Wspeed) (ID)	284.118	0.057
(Solar*Wspeed) (Rh*Wspeed) (ID)	294.383	0.001

Finally, the conditional-logistic, resource-selection function stratified by individual deer was significant (P = 0.004, AIC_C = 1,823), and indicated that a point in or near live-oak cover was more likely to be a deer location than a random point (hazard ratio = 1.546). We then calculated similar resource-selection functions after dividing these data into two subsets: calm, where wind speed was $\leq$ the median value (102 m * min^{-1}); and windy, where wind speed was > the median value. When it was windy, habitat was not a significant predictor of deer locations versus random points (P > 0.05). When it was calm, not only was habitat a significant predictor (P = 0.035), but the model preformed substantially better (AIC_C = 775) than did the model for all wind conditions (ΔAIC_C = 1,823 - 775 = 1,048).

DISCUSSION

We tested the role of weather variables in the process by which black-tailed deer select resources; clearly, such variables can influence those decisions. Even our coarse analysis of resource selection highlighted the influence of weather conditions in understanding the ecology of black-tailed deer during winter. Our observations hold import for biologists and managers studying habitat selection for large herbivores where only measures of vegetation or topographic features are gathered. Additional information on the thermal environment may provide further insights into the ecology and behavior of these large herbivores.

We acknowledge that our retrospective analysis involved data initially collected for other purposes. These data, however, were appropriate for testing hypotheses concerning the role of weather variables in resource selection by black-tailed deer. Our analyses are especially timely because of new information linking the role of the thermal environment to the ecology of large mammals (Natori and Porter 2007). We also used coarse descriptions of habitats, conservative estimates of environmental influences on deer from our black-body devices, and traded-off small sample size of deer to obtain detailed environmental measurements in the primary habitats of these large herbivores. We did, however, use a statistical design (conditional logistic regression) that allowed us to use all of our sampling locations while avoiding pseudoreplication (Boyce and McDonald 1999, Boyce 2006). Despite all of these difficulties, including an accompanying lack of statistical power, we documented that abiotic conditions influenced habitat use and selection by black-tailed deer. If these difficulties were going to negatively influence our analyses, we should have failed to detect effects of weather on habitat selection—we obtained the opposite pattern.

Measures of resource selection can be extremely sensitive to scale (Bowyer and Kie 2006). We obtained a median error associated with deer locations of ~ 150 m. Some GPS collars provide more accurate locations than VHF systems we used, but are by no means free from error (Villepique et al. 2008). Our telemetry error was similar to that of other investigators who were able to detect habitat selection by mule deer (Nicholson et al. 1997, Stewart et al. 2002). Buffering habitats rather than deer locations yields the same analytical approach, and allows a more sophisticated statistical design. Moreover, Kie et al. (2002) documented that mule deer and black-tailed deer made decisions about habitat selection at scales far larger than their home ranges. Consequently, we believe our sampling scale was reasonable; telemetry error (and subsequent buffering of habitats) did not influence our ability to detect resource selection by black-tailed deer.

Weather data are likely to become increasingly important for understanding the ecology of ungulates, especially under changing and variable weather conditions (Post and Stenseth 1999, Forchhammer et al. 2002, Lenart et al. 2002, Dussault et al. 2004). Rachlow and Bowyer (1998) documented substantial differences in habitat selection by maternal Dall's sheep, Ovis dalli, in years with markedly dissimilar precipitation, temperature, and consequently forage availabilities. Bowyer et al. (1998) concluded that the thermal environment was a critical component of birth-site selection by neonatal black-tailed deer, and Bowyer et al. (1999) noted the importance of south-facing slopes in birth-site selection by moose, Alces alces. Further, Andrew et al. (1999) described seasonal differences in selection of aspect by bighorn sheep, Ovis canadensis, in a Sonoran desert environment. We could not test for effects of aspect on resource selection by black-tailed deer because our study areas had little topographic relief. This is an area for future research.

Mule deer can exhibit hyperthermia when air temperatures exceed 20° C during summer and 5° C during winter (Parker and Robbins 1984), although animal response may vary among populations and across broad geographic areas (Mysterud and Østbye 1999). Moreover, mule deer seek daytime beds that provide refuge from solar radiation on hot, clear days (Sargeant et al. 1994). In our study, open habitats where animals were exposed to more sunlight were warmer during the day and cooler at night than areas in or near live-oak cover (Fig. 2). We hypothesize these patterns were related to the absorption of solar radiation during the day and back radiation to open sky on clear nights in habitats other than live-oak cover. Correspondingly, deer were located in or near live-oak cover 80% of the time during daylight hours. The most parsimonious models indicated that wind speed in particular, as well as air temperature, solar radiation, relative humidity, and interactions between those variables likely play roles in determining whether deer occur in or near live-oak cover or in other more open habitats (Table 1). Further, resource-selection functions used to distinguish between deer locations and random points based on habitat type performed best when limited to calm days with low wind speeds.

Food and water may be important components of habitat selection by mule deer (Bowyer 1984, 1986, Boroski and Mossman 1996, Stewart et al. 2002). Water, however, is unlikely to be a critical component of resource selection by mule deer during winter (Bowyer 1986). Likewise, seasonal changes in activity patterns of mule deer, including foraging behavior, are well documented (Bowyer and Kie 2004). Nonetheless, our best resource-selection models were for calm days only, an outcome that is hard to reconcile with the foraging ecology of deer. This interpretation for habitat selection would have deer seeking food or water in live-oak habitat only under calm conditions. Consequently, we believe the most parsimonious explanation for black-tailed deer in winter pelage using live-oak thickets was to ameliorate heat gain on calm, warm days with low humidity.

Although relationships between black-body temperatures, air temperature, and solar radiation were among the strongest we detected, wind speed and its interaction with relative humidity were the best predictors of where deer occurred. Wind speed was positively correlated with group size in southern mule deer, O. h. fuliginatus, with large groups in open meadows ostensibly acting as a mechanism to reduce the risk of predation under windy conditions (Bowyer et al. 2001). Such gregarious behavior might be particularly useful when the detection of an approaching predator by deer was hampered by wind noise and moving vegetation (Bowyer et al. 2001). We hypothesize that use of live-oak cover and nearby areas by black-tailed deer (Fig. 1) primarily during periods of low wind may reflect their relative inability under windy conditions to detect approaching stealthy predators, such as mountain lions, Puma concolor (Pierce et al. 2000a, 2000b). Moreover, deer spending less time in live-oak cover at night than during the day may further reflect avoidance of mountain lions, which hunt primarily at night (Pierce et al. 2000a, 2000b, 2004). We cannot distinguish between these hypotheses, but note that they need not be mutually exclusive. The critical point from our analysis is that weather variables influenced behavior and habitat selection of deer, whether through ameliorating heat gain on calm, warm days or limiting risk of predation. The failure to consider environmental variables in studies of resource selection could lead to an incomplete understanding of the ecology of these large herbivores.

Our findings indicate that additional research on the role of the thermal environment in resource selection by large herbivores is warranted. Several fruitful topics for further study include understanding differing life-history strategies between sexes, and the fitness consequences of resource selection. For instance, mule deer exhibit sexual dimorphism in size (Weckerly 1998), and the sexes segregate from one another for much of the year (Bowyer 1984, 2004). Obtaining a more complete knowledge of how larger males cope with weather variables and how they differ from responses of smaller females is a logical next step; initial findings indicate this may be important (Conradt et al. 2000). Moreover, investigating the fitness consequences of resource selection (Farmer et al. 2006) is critical to understanding the response of large herbivores to a changing climate and how such changes relate to the population dynamics of these unique mammals (Post and Stenseth 1999, Forchhammer et al. 2002). We suggest that additional studies are necessary to understand how weather variables and thermal landscapes influence resource selection by deer and other large herbivores, and hope that our research has provided an initial step in that direction.

ACKNOWLEDGMENTS

This study was funded by the Pacific Southwest Research Station of the U. S. Forest Service, the California Department of Fish and Game, and the Department of Biological Sciences at Idaho State University. We thank B. B. Boroski for coordinating the collection of field data. D. P. Anderson and two reviewers made helpful comments on this manuscript.

LITERATURE CITED

Ager, A. A., B. K. Johnson, J. W. Kern, and J. G. Kie. 2003. Daily and seasonal movements and habitat use by female Rocky Mountain elk and mule deer. Journal of Mammalogy 84:1076-1088.

Andrew, N. G., V. C. Bleich, and P. V. August. 1999. Habitat selection by mountain sheep in the Sonoran desert: implication for conservation in the United States and Mexico. California Wildlife Conservation Bulletin 12:1-30.

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

Bakken, G. S. 1992. Measurement and application of operative and standard operative temperatures in ecology. American Zoologist 32:194-216.

Boroski, B. B., and A. S. Mossman. 1996. Distribution of mule deer in relation to water sources in northern California. Journal of Wildlife Management 60:770-776.

Bowyer, R. T. 1984. Sexual segregation in southern mule deer. Journal of Mammalogy 65: 410-417.

Bowyer, R. T. 1986. Habitat selection by southern mule deer. California Fish and Game 72:153-169

Bowyer, R. T. 2004. Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation and management. Journal of Mammalogy 85: 1039-1052.

Bowyer, R. T., and J. G. Kie. 2004. Effects of foraging activity on sexual segregation in mule deer. Journal of Mammalogy 85:498-504.

Bowyer, R. T., and J. G. Kie. 2006. Effects of scale on interpreting life-history characteristics of ungulates and carnivores. Diversity and Distributions 12:244-257.

Bowyer, R. T., J. G. Kie, and V. Van Ballenberghe. 1998. Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? Journal of Mammalogy 79: 415-425.

Bowyer, R. T., D. R. McCullough, and G. E. Belovsky. 2001. Causes and consequences of sociality in mule deer. Alces 37:371-402.

Bowyer, R. T., V. Van Ballenberghe, J. G. Kie, and J. A. K. Maier. 1999. Birth-site selection by Alaskan moose: maternal strategies for coping with a risky environment. Journal of Mammalogy 80:1070-1083.

Boyce, M. S. 2006. Scale for resource selection functions. Diversity and Distributions 12:269-276.

Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14:268-272.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Conradt, L., T. H. Clutton-Brock, and F. E. Guinness. 2000. Sex differences in weather sensitivity can cause habitat segregation: red deer as an example. Animal Behaviour 59:1049-1060.

Cook, J. G., L. L. Irwin, L. D. Bryant, R. A. Riggs, and J. W. Thomas. 1998. Relations of forest cover and condition of elk: a test of the thermal cover hypothesis in summer and winter. Wildlife Monographs 141:1-61.

Dussault, C., J. P. Ouellet, R. Courtois, J. Hout, L. Breton, and J. Larochelle. 2004. Behavioural responses of moose to thermal conditions in the boreal forest. Écoscience 11:321-328.

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

Farmer, C. F., D. K. Person, and R. T. Bowyer. 2006. Risk factors and survivorship of black-tailed deer in a managed forest landscape. Journal of Wildlife Management 70:1403-1415.

Forchhammer, M. C., E. Post, N. C. Stenseth, and D. M. Boertmann. 2002. Long-term responses in arctic ungulate dynamics to changes in climatic and trophic processes. Population Ecology 44:113-120.

Kie, J. G., and B. B. Boroski. 1995. The effects of cattle grazing on black-tailed deer during winter on the Tehama Wildlife Management Area. U.S. Forest Service Report PSW-89-CL-030.

Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology 83:530-544.

Lenart, E. A., R. T. Bowyer, J. Ver Hoef, and R. W. Ruess. 2002. Climate change and caribou: effects of summer weather on forage. Canadian Journal of Zoology 80:664-687.

Mysterud, A., and E. Østbye. 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. Wildlife Society Bulletin 27:385-394.

Natori, Y., and W. P. Porter. 2007. Model of Japanese serow (*Capricornis crispus*) energetics predicts distribution on Honshu, Japan. Ecological Applications 17:1441-1459.

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.

Parker, K. L., and M. P. Gillingham. 1990. Estimates of critical thermal environments for mule deer. Journal of Range Management 43:73-81.

Parker, K. L., and C. T. Robbins, 1984. Thermoregulation in mule deer and elk. Canadian Journal of Zoology 62:1409-1422.

Pierce, B. M., V. C. Bleich, and R.T Bowyer. 2000a. Selection of mule deer by mountain lions and coyotes: effects of hunting style, body size, and reproductive status. Journal of

Mammalogy 81:462-472.

Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000b. Social organization of mountain lions: does a land tenure system regulate population size? Ecology 81:1533-1543.

Pierce, B. M., V. C. Bleich, and R.T. Bowyer. 2004. Habitat selection by mule deer: forage benefits or risk of predation? Journal of Wildlife Management 68:533-541.

Porter, W. P., J. L. Sabo, C. R Tracy, O. J. Reichman and N. Ramankutty. 2002. Physiology on a landscape scale: plant-animal interactions. Integrative Comparative Biology 42:431-453.

Post, E., and N. C. Stenseth. 1999. Climatic variability, plant phenology, and northern ungulates. Ecology 80:1322-1339.

Rachlow, J. L., and R. T. Bowyer. 1998. Habitat selection by Dall's sheep (*Ovis dalli*): maternal trade-offs. Journal of Zoology London 245:457-465.

Renecker, L. A., and R. J. Hudson. 1986. Seasonal energy expenditures and thermoregulatory response in moose. Canadian Journal of Zoology 64:322-327.

Sargeant, G. A., L. E. Eberhardt, and J. M. Peek. 1994. Thermoregulation by mule deer (*Odocoileus hemionus*) in arid rangelands of southcentral Washington. Journal of Mammalogy 75:536-544.

SAS Institute. 1999. SAS/STAT user's guide, version 8. SAS Publishing, Cary, North Carolina, USA.

Schemnitz, S. D. 1994. Capturing and handling wild animals. Pages 106-124 *in* T. A. Bookhout, editor. Research and management techniques for wildlife and habitats. The Wildlife Society, Bethesda, Maryland, USA.

Stewart, K. M., R. T. Bowyer, J. G. Kie, N. J. Cimon, and B. K. Johnson. 2002. Temprospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. Journal of Mammalogy 83:229-244.

Villepique, J. T., V. C. Bleich, R. A. Botta, B. M. Pierce, T. R. Stephenson, and R. T. Bowyer. 2008. Evaluating GPS collar error: a critical evaluation of Televilt POSREC-Science™ collars and a method for screening location data. California Fish and Game 94:155-168.

Weckerly, F. W. 1998. Sexual size dimorphism: influence of mass and mating systems in the most dimorphic mammals. Journal of Mammalogy 79:33-52.

Received: 8 December 2008
Accepted: 9 March 2009