

Short communication

Potential thermoregulatory advantages of shade use by desert bighorn sheep

J.W. Cain^{*,1}, B.D. Jansen², R.R. Wilson³, P.R. Krausman⁴

School of Natural Resources, University of Arizona, 325 Biological Sciences East, Tucson, AZ 85721, USA

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Abstract

Ungulates in arid climates use a variety of mechanisms to cope with environmental conditions that can result in heat stress and dehydration. Use of shade during midday is common among desert ungulates of the southwestern United States. Desert bighorn sheep (*Ovis canadensis mexicana*) use both vegetation and caves as sources of thermal cover. We assessed potential thermoregulatory advantages of the use of vegetation and caves by desert bighorn sheep on the Cabeza Prieta National Wildlife Refuge, Arizona. Midday ambient temperatures in caves were an average of 6.9 °C (SE = 0.344) lower than control sites; ambient temperature under tree canopies was an average of 3.3 °C (SE = 0.950) below control sites. Caves provided higher quality shade than tree canopies; midday temperature in caves was an average of 3.4 °C (SE = 1.06) lower than under tree canopies. Potential thermal benefits of both caves and tree canopies increased with increasing daily high temperature. Behavioral adaptations function in combination with physiological and morphological mechanisms and are of critical importance for the maintenance of temperature and water balance. Short-term physiological and ecological performance is influenced by habitat selection and use of microhabitat; abiotic factors (e.g., ambient temperature) can ultimately influence animal fitness and the demography of animal populations.

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1. Introduction

Ungulates in arid climates are challenged with maintaining body temperature within physiologically acceptable limits and minimizing water loss (Feldhamer et al., 1999). In response to these environmental factors, ungulates adapted to deserts use a variety of physiological, morphological, and behavioral

*Corresponding author. Tel.: +1 271 11 717 6410; fax: +1 271 11 403 1429.

E-mail address: jwcain@ag.arizona.edu (J.W. Cain).

¹Present address: Centre for African Ecology, School of Animal, Plant, and Environmental Sciences, University of the Witwatersrand, Private bag 3, Wits 2050, Johannesburg, South Africa.

²Present address: Department of Wildlife and Fisheries Sciences South Dakota State University, P.O. Box 1822, Rapid City, SD 57709-1822, USA.

³Present address: Department of Wildland Resources, Utah State University, 5230 Old Main Hill, Logan, UT 84322, USA.

⁴Present address: College of Forestry and Conservation, Wildlife Biology Program, 32 Campus Drive, Forestry Building, University of Montana, Missoula, MT 59812, USA.

mechanisms to cope with environmental conditions that can result in heat stress and dehydration (Cain et al., 2006; Louw and Seely, 1982; Schmidt-Nielsen, 1979).

Behavioral adaptations function in combination with physiological and morphological mechanisms and are of critical importance for the maintenance of temperature and water balance within physiologically acceptable limits (Bartholomew, 1964). Restricting of daily activities to time periods that reduce daily heat loads and water loss, diet selection, use of microhabitats, and body orientation are behaviors commonly used by desert ungulates for maintaining temperature and water balance (Berry et al., 1984; Cain et al., 2006; Sargeant et al., 1994).

During the hottest, driest periods of the year, desert ungulates tend to spend a smaller proportion of daytime hours being active and shift their activity patterns to crepuscular and nocturnal periods (Alderman et al., 1989; Jarman, 1973, 1977; Sargeant et al., 1994; Vrahimis and Kok, 1992; Wilson, 2006). In addition, animals commonly spend their inactive periods using cooler microclimates (Lewis, 1978; Ostrowski et al., 2003; Tull et al., 2001; Wilson, 2006) or forage in shaded areas (Matson et al., 2005; Owen-Smith, 1998).

Use of shaded microhabitat during midday when temperatures are highest is a common behavior among desert ungulates of the arid southwestern United States, including, desert bighorn sheep (*Ovis canadensis mexicana*, *O. c. nelsoni*, *O. c. weemsii*), desert mule deer (*Odocoileus hemionus eremicus*), Sonoran pronghorn (*Antilocapra americana sonoriensis*), and collared peccary (*Pecari tajacu*) (Anthony, 1972; Krausman et al., 1999; Sowls, 1997; Tull et al., 2001; Wilson, 2006). These species seek vegetation with a dense canopy during the heat of midday and are commonly observed using shade created by vegetation. When available, caves are an additional source of thermal cover. Due to the nature of their habitat, desert bighorn sheep often have caves more readily available than other species of desert ungulate (e.g., Sonoran pronghorn, desert mule deer) and they commonly use caves as sources of thermal cover (Hansen, 1980; Simmons, 1969a, b, 1980; J.W. Cain, personal observation). However, other desert ungulates (e.g., white-tailed deer (*Odocoileus virginianus carminis*), collared peccary (*P. tajacu*)) also use caves when available (Krausman, 1979).

Although use of caves by desert bighorn sheep has been reported, potential thermoregulatory benefits of cave use have not been quantified. Our objectives were to assess the potential thermoregulatory advantages of the use of caves as thermal cover by desert bighorn sheep and to quantify the differences in the potential thermal load experienced by desert bighorn using caves for thermal cover relative to unshaded areas, and to compare potential thermal benefits provided by caves and trees in desert bighorn sheep habitat.

2. Materials and methods

2.1. Study area

We conducted this study on Cabeza Prieta National Wildlife Refuge (CPNWR), Arizona, USA. Topography consisted of a series of rugged mountain ranges surrounded by wide alluvial valleys; elevations ranged from 200 to 900 m. The study sites were located in the Sierra Pinta (32.26263°N, 113.54157°W) and Cabeza Prieta Mountains (32.34915°N, 113.82309°W); each mountain range was inhabited by a population of 60–100 desert bighorn sheep (Cain and Krausman, unpublished data). Climate of CPNWR was arid; annual precipitation occurred in a bimodal pattern, with peaks during summer from monsoon thunderstorms and during winter rains. Long-term mean annual precipitation in the area (1969–2005, Tacna, Arizona approximately 64 km north of study area) was 105 mm. During summer, temperatures often exceeded 45 °C; average low temperature was 22.3 °C (Western Regional Climate Data Center, 2005). Winters were mild with a mean daily high temperature of 21.1 °C and mean daily low temperature of 2.6 °C (Western Regional Climate Data Center, 2005). Vegetation was typical of the Lower Colorado River Valley subdivision of Sonoran deserts scrub. Valleys are characterized by plains of creosote bush (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), and ocotillo (*Fouquieria splendens*), with ironwood (*Olneya tesota*), blue palo verde (*Parkinsonia florida*), and triangle-leafed bursage (*A. deltoidea*) common along washes. Vegetation in mountains was characterized by ironwood, catclaw acacia (*Acacia greggii*), foothill palo verde (*Parkinsonia microphyllum*), creosote bush, white bursage, ratany (*Krameria* spp.), brittlebush (*Encelia farinosa*), elephant tree (*Bursera microphylla*), and mallow (*Sphaeralcea* spp. and *Hibiscus* spp.). Common grasses and forbs included three-awn (*Aristida* spp.), grama (*Bouteloua* spp.), big galleta grass (*Pleuraphis rigida*), Indian wheat (*Plantago patagonica*), and scorpionweed (*Phacelia ambigua*) (Simmons, 1966; Turner and Brown, 1994).

Common cacti included giant saguaro (*Cereus giganteus*), barrel cactus (*Ferocactus* spp.), pincushion cactus (*Mammillaria* spp.), teddy bear cholla (*Cylindropuntia bigelovii*), and buckhorn cholla (*C. acanthocarpa*). Plant nomenclature follows Felger (1998).

2.2. Data collection and analysis

To determine the potential thermoregulatory benefits that could be experienced by desert bighorn sheep using caves during summer we compared the potential thermal load inside caves with potential thermal load in unshaded areas <100 m outside the cave. Because differences in humidity can influence rates of evaporative water loss in animals and thereby influence thermoregulation and water balance, we also measured humidity inside and outside of caves. In addition, we also monitored potential thermal load and humidity under the canopy of mature palo verde and ironwood trees <100 m from caves.

We identified areas within the Sierra Pinta and Cabeza Prieta Mountains with caves that were used as thermal cover by desert bighorn sheep. Within these areas, we selected caves located on north facing slopes as potential sampling locations. Studies of desert bighorn sheep habitat selection have documented preferential use of north facing slopes during the summer (Alvarez-Cárdenas et al., 2001; Tarango, 2000). In addition, we commonly observed desert bighorn sheep using caves on north facing slopes and we believed that these would provide the best shade, and therefore confer the greatest thermoregulatory advantage to sheep. We only sampled caves that contained bighorn sheep tracks or fresh (i.e., ≤ 2 months old) pellets.

To monitor potential thermal loads and humidity, we programmed 4 HOBO RH data loggers (Onset Computer Corporation, Bourne, Massachusetts, USA) to record temperature and absolute humidity (g/m^3) hourly. We attached HOBO data loggers at the top of a 46 cm long surveyor's stake using an "L" bracket. We placed one data logger in each cave, one immediately outside of the cave (control), and one in shade of a palo verde or ironwood tree near the cave; all data loggers were located approximately 46 cm above ground level. To minimize the influence of potential variation in temperature and humidity measurements between individual data loggers we randomized placement (i.e., cave, tree, control) of the four data loggers. We monitored eight caves and five trees during summers (May–September) of 2004 and 2005. Because our primary interest was potential thermal advantages of cave use during the most thermally stressful periods, we limited our sampling to summer months. We further limited our analysis to the midday period from 11:00 to 17:00 because ambient temperatures are highest and cave use by desert bighorn sheep is greatest during this time.

We did not measure dry-bulb temperature or control for the influence of direct or reflected solar radiation on the measurement of temperature differences between the test locations (e.g., cave vs. unshaded sites). It is likely that our measurements included the influence of radiation on temperature readings, particularly for the unshaded test locations. Therefore, we consider the temperature measurements recorded by the data loggers to be a proxy for the potential thermal load, including the components of the thermal load contributed by air temperature and solar radiation, which would be experienced by desert bighorn sheep using these locations. We do not consider our temperature readings to reflect exact measures of dry-bulb temperature. Given our methodology, there are limitations in the conclusions we can make regarding the realized thermal advantages resulting from cave use by desert bighorn sheep which can only be overcome by monitoring the body temperature of desert bighorn sheep and estimating heat exchange between the animal and its environment, including the influence of radiation, conduction, and convection on heat exchange rates (Porter and Gates, 1969). However, other studies have found that body temperature is highly correlated with ambient temperature (Fuller et al., 1999, 2005; Jessen and Kuhnen, 1996; Parker and Robbins, 1984). Therefore we believe that ambient temperatures we recorded are an adequate proxy for potential thermal loads experienced by desert bighorn sheep.

To compare potential thermal loads between different microhabitats we calculated the difference in hourly temperature and absolute humidity between data loggers located in caves, under trees, and controls (i.e., cave—control, tree—control, and cave—tree). We used a one-sample *t*-test to test whether the mean difference in temperature and humidity between the cave and tree locations and their respective control locations was significantly different from zero (Zar, 1999). To examine the variation in shade quality between caves and trees we used a one-sample *t*-test to test whether the mean difference in temperature and humidity between caves and corresponding tree locations was significantly different from zero. To determine if potential thermal benefits of

shade use varied with maximum daily temperature, we calculated maximum daily temperature for each day at the control locations and mean temperature difference between cave and control sites and tree and control sites for each day. We then used linear regression to test the relationship between maximum daily temperature and mean daily temperature difference between cave sites and control sites and tree and control sites.

3. Results

Ambient temperature at control locations during midday was highest during July (mean = 44.8 °C, SD = 2.8) and August (mean = 42.2 °C, SD = 3.2), followed by June (mean = 41.5 °C, SD = 5.5) and September (mean = 40.5 °C, SD = 3.8), with May (mean = 38.3 °C, SD = 4.6) having the lowest mean temperature during midday (Fig. 1a). Absolute humidity was lowest in May (mean = 6.02 g/m³, SD = 2.12) and June (mean = 6.24 g/m³, SD = 2.48), then increased during July (mean = 9.98 g/m³, SD = 3.14), August

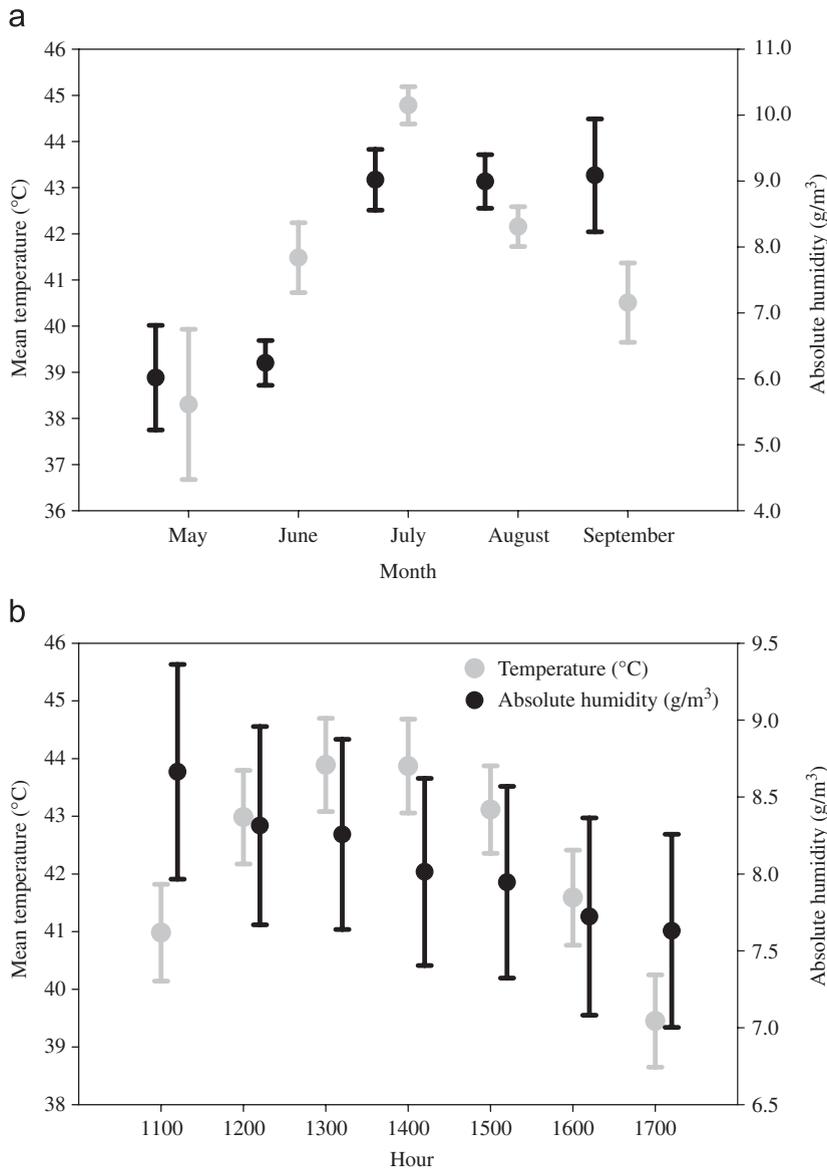


Fig. 1. Mean (\pm 95% confidence interval) monthly (a) and hourly (b) ambient temperature and relative humidity at control locations during summer (May–September 2004, 2005), Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona.

(mean = 8.99 g/m³, SD = 3.03), and September (mean = 9.09 g/m³, SD = 3.77; Fig. 1a). Mean hourly ambient temperature at control locations during midday increased from 11:00 (mean = 40.9 °C, SD = 4.3) to 12:00 (mean = 42.9 °C, SD = 4.2), peaked at 13:00 (mean = 43.9 °C, SD = 4.1) to 14:00 (mean = 43.9 °C, SD = 4.1), then declined from 15:00 to 17:00 (15:00, mean = 43.1 °C, SD = 3.9; 16:00, mean = 41.6 °C, SD = 4.1; 17:00, mean = 39.5 °C, SD = 4.03). Mean hourly absolute humidity was highest at 11:00 (mean = 8.66 g/m³, SD = 3.56), then declined gradually until 17:00 (12:00, mean = 8.31 g/m³, SD = 3.31; 13:00, mean = 8.26 g/m³, SD = 3.15; 14:00, mean = 8.01 g/m³, SD = 3.09; 15:00, mean = 7.95 g/m³, SD = 3.15; 16:00, mean = 7.72 g/m³, SD = 3.22; 17:00, mean = 7.63 g/m³, SD = 3.16; Fig. 1b).

The potential thermal load in caves was always lower than that at control sites during midday; hourly temperature difference between caves and control sites ranged from -4.1 to -8.9 °C (Fig. 2a). Potential thermal load under tree canopies was lower than that at control sites from 11:00 until 16:00 (Fig. 2a). The hourly difference between trees and control sites ranged from -0.72 to -4.7 °C below control sites. During midday, cave temperature was an average of 6.9 °C (SE = 0.344) lower than control sites ($t_{1, 7} = -20.145$, two-sided $P < 0.001$). Average absolute humidity did not differ between caves (mean = 6.46 g/m³, SE = 0.518) and control sites (mean = 6.17 g/m³, SE = 0.651; $t_{1, 7} = 0.958$, two-sided $P = 0.370$; Fig. 2b). Temperature under tree canopies was an average of 3.3 °C (SE = 0.950) lower than control sites ($t_{1, 4} = -3.453$, two-sided $P = 0.026$); mean absolute humidity did not differ between tree (mean = 6.13 g/m³, SE = 0.662) and control sites (mean = 6.09 g/m³, SE = 0.663; $t_{1, 4} = 0.472$, two-sided $P = 0.661$). Caves

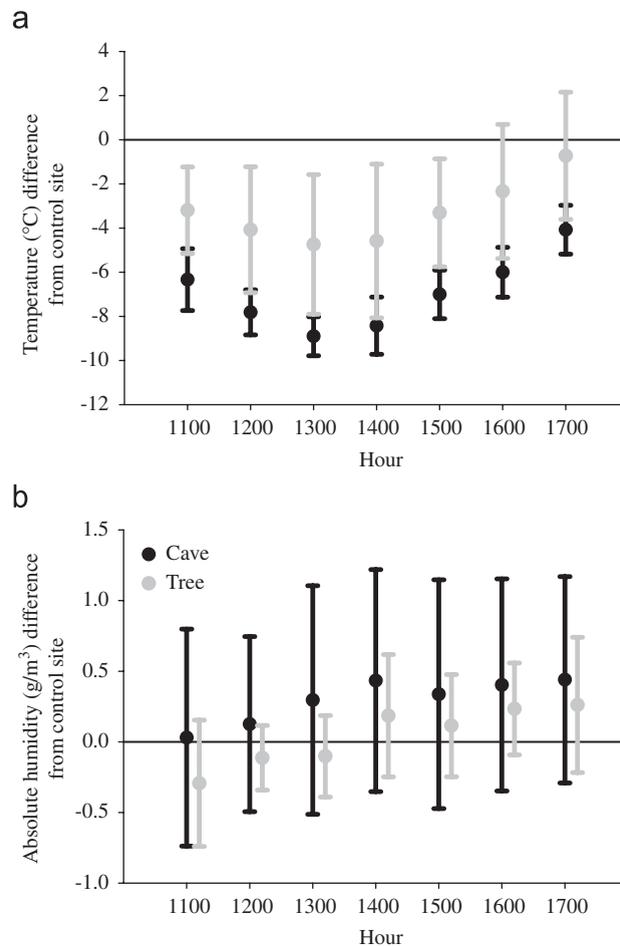


Fig. 2. Mean difference in hourly temperature (a) and relative humidity (b) between cave and control locations and tree and control locations during summer (May–September 2004, 2005), Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona.

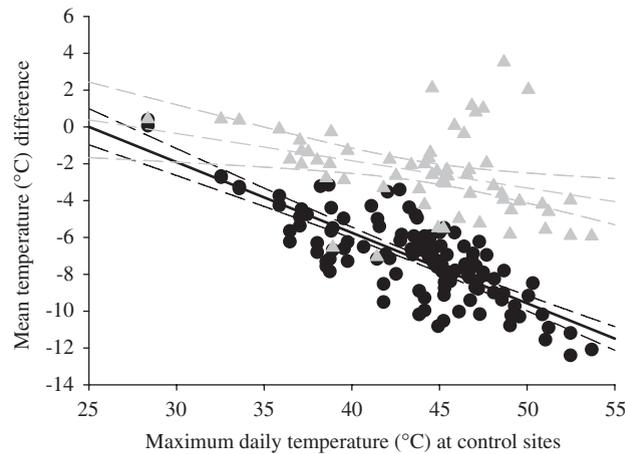


Fig. 3. Least-squares linear regression lines and 95% confidence intervals for the mean hourly temperature difference between caves and control sites (●), and trees and control sites (▲) and the maximum daily temperature at control sites during summer (May–September 2004, 2005), Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona.

provided more shade than tree canopies. The mean temperature during midday was an average of 3.4°C (SE = 1.06) lower in caves than under tree canopies ($t_{1,8} = -3.21$, two-sided $P = 0.018$). The temperature difference between caves and tree canopies ranged from 2.9 to 3.7°C depending on the time of day. Whereas the mean absolute humidity did not differ between caves and trees ($t_{1,8} = 1.12$, $P = 0.304$).

The magnitude of the difference in potential thermal load between cave and control sites increased with increasing daily high temperature at control sites (Fig. 3). The temperature difference between cave and control sites increased by approximately 0.4°C with each 1°C increase in the maximum daily high temperature ($\beta = -0.386 \pm 0.026$, $t_{1,120} = -14.923$, $P < 0.001$; Fig. 3). Likewise, the temperature difference between tree sites and control sites increased with increasing daily high temperature, although at a slower rate than the difference between cave and control sites (Fig. 3); temperature difference between shade under tree canopies and control sites increased by 0.14°C with every 1°C increase in the maximum daily high temperature ($\beta = -0.148 \pm 0.052$, $t_{1,60} = -2.832$, $P = 0.006$; Fig. 3). Hence the potential thermal benefits of shade use in both caves and under trees by desert bighorn sheep increased with higher maximum daily temperature.

4. Discussion and conclusions

Potential thermal loads have been found to be 2–4 times higher in the sun than in shaded microclimates (Kamau and Maloiy, 1985; Zahn, 1985). The amount of time spent in shaded areas during the day increases with increasing ambient temperatures (Ostrowski et al., 2003). In the Silver Bell Mountains, Arizona, desert bighorn sheep were found bedded in the shade during midday (i.e., 11:00–17:00) approximately 43% and 85% of the time during the cool seasons and hot seasons, respectively (B.D. Jansen, unpublished data). Simmons (1969b) found that desert bighorn spent an average of 7 h/day bedded in the shade during hot periods compared with only 0.75 h/day during winter.

The use of shaded microclimates reduces heat load, helps maintain a temperature gradient between the body and the environment that is conducive for convective heat loss, thereby reducing the need for evaporative cooling and minimizing evaporative water loss (Finch, 1972; Kamau and Maloiy, 1985; Ostrowski et al., 2003). Mean ambient temperature in caves throughout the midday period was lower than the normal body temperature (ca. 39°C) of bighorn sheep. Therefore, desert bighorn sheep using caves during the midday period experienced a favorable thermal gradient that facilitated non-evaporative, convective heat loss and minimized evaporative water loss. In addition, bedding on cool substrates can facilitate conductive heat loss (Jacobsen, 1979). During midday, temperature of cave surfaces is much cooler than the surface of surrounding unshaded areas (B.D. Jansen, J.W. Cain, and P.R. Krausman, personal observations). However, because we did not measure surface temperatures, we cannot estimate the magnitude of the thermal gradient between

bighorn sheep and surface of the cave. According to Simmons (1969b), the surface of shaded areas used by bighorn sheep during summer in the Sierra Pintada was an average of 7.8 °C lower than nearby unshaded areas (Simmons, 1969b).

By using caves as midday bed sites during summer months, desert bighorn sheep are exposed to significantly lower potential thermal loads (e.g., 4–9 °C lower) than those in unshaded areas and 4 °C lower than shaded areas under tree canopies. The relationship between the magnitude of the difference in the potential thermal loads between caves and unshaded areas indicates that potential thermal advantages of caves used by desert bighorn sheep are greatest at the highest ambient temperatures. Our observations of desert bighorn sheep in various mountain ranges corroborate these findings. In mountain ranges that have abundant caves, bighorn sheep were rarely observed bedded under tree canopies during midday, whereas in mountain ranges where caves are absent, bighorn sheep frequently bed under tree canopies (B.D. Jansen, J.W. Cain, and P.R. Krausman, personal observations). Approximately, 89% of the bighorn sheep we observed bedded during midday period of the summer months were bedded in caves (J.W. Cain and P.R. Krausman, unpublished data). Simmons (1969b) also documented a preference by desert bighorn sheep for caves as midday bed sites during hot months. Additionally, 90% of the observations of desert bighorn sheep on the CPNWR between 12:00 and 17:00 on hot days were bedded in the shade (Simmons, 1969b).

Thermal conditions influence activity budgets of many ungulate species and high thermal loads can constrain foraging time. During periods of high ambient temperature, ungulates can experience reductions in the total foraging time and daily energy gain (Belovsky and Slade, 1986). Some ungulates are able to maintain total foraging time by shifting feeding to crepuscular or nocturnal periods when thermal loads are lower (Owen-Smith, 1998; Simmons, 1969b). Although, shifting foraging time may allow some ungulates to maintain daily energy gain, it may also place them at greater risk of predation. For example, the major predators of desert bighorn sheep, mountain lion (*Felis concolor*), bobcat (*Lynx rufus*), and coyote (*Canis latrans*), are crepuscular and nocturnal (Anderson and Lovallo, 2003; Bekoff and Gese, 2003; Pierce and Bleich, 2003). Therefore, short-term physiological and ecological performance of an animal is greatly influenced by habitat selection and use of microhabitat (Ames, 1980; Huey, 1991). The influence of abiotic factors, such as caves, can ultimately influence animal fitness and the demography of animal populations.

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