Responses of Desert Bighorn Sheep to Removal of Water Sources

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ABSTRACT In arid regions of the southwestern United States, water is often considered a primary factor limiting distribution and productivity of desert ungulates, including desert bighorn sheep (*Ovis canadensis mexicana*). Thus, wildlife management agencies and sportsmen's organizations have invested substantial time and resources in the construction and maintenance of water catchments. Although the availability of freestanding water sources is believed to influence many aspects of the ecology of desert bighorn sheep, the efficacy of these water sources has been questioned and has not been examined experimentally. We used a before-after–control-impact study design to determine if removal of water catchments changed diet, characteristics of foraging areas used by female desert bighorn sheep, home-range size, movement rates, distance to catchments, adult mortality, productivity, or juvenile recruitment in 2 mountain ranges on the Cabeza Prieta National Wildlife Refuge, Arizona, USA. During pretreatment (2002–2003), we ensured that water catchments were available to desert bighorn sheep in both mountain ranges; during posttreatment (2004–2005), we drained all water catchments in the treatment range. We measured diet composition, characteristics of foraging areas, 50% and 95% kernel home ranges, movement rates, and distance to water catchments seasonally from 2002 to 2005. We also estimated adult survival, lamb:female, and yearling:female ratios from 2002 to 2005. We predicted that removal of water catchments would result in 1) increased use of foraging areas with more vegetation cover, more thermal cover, and higher succulent abundance; 2) increased consumption of cacti and other succulents; 3) an increase in home-range size, movement rates, and distance to nearest catchment; and 4) a decrease in adult survival, productivity, and juvenile recruitment. Removal of water catchments in the treatment range did not result in predicted changes in diet, foraging area selection, home-range size, movement rates, mortality, productivity, or recruitment. Female desert bighorn sheep did use areas with more thermal cover during the summer after removal of water catchments, but other characteristics of foraging areas used by bighorn sheep and their diet did not change appreciably with removal of water catchments. We did not document changes in home-range area, movement rates, or distance sheep were from water during hotter months; we only documented changes in home-range area, movement rates, and distance to water catchments during winter and autumn. There were 10 desert bighorn sheep mortalities in the treatment range and 8 in the control range; 7 mortalities in each mountain range were during pretreatment. Twelve of the 18 total mortalities occurred during summer. Survival rate was lower during pretreatment than posttreatment in both mountain ranges. We did not document increased mortality or a change in lamb:female or yearling:female ratios after removal of water catchments. Home-range area and movement rates declined with increasing precipitation. Annual survival rates increased with increases in the current year's total precipitation and total precipitation during the previous year; annual survival rates declined with increases in average daily temperature during winter. There was a severe drought during pretreatment and abnormally wet conditions during posttreatment. The increase in precipitation that coincided with removal of water sources improved forage conditions during posttreatment and may have provided adequate water for female desert bighorn sheep. The lack of change in home-range size, movement rates, and distance to the nearest water catchment during hot, dry seasons after removal of water sources suggests that forage conditions played a greater role in determining home-range area and movement rates than did the presence of water catchments. Higher mortality rates during the drought of the pretreatment period indicates that during droughts as severe as that of 2002, presence of water catchments was not sufficient to prevent mortalities of desert bighorn sheep and a lack of forage quality and quantity was likely the primary limiting factor of the population during this time. Improving forage conditions during posttreatment, increases in forage moisture content, and availability of naturally occurring sources of free water in the treatment range likely minimized any impact of removing water catchments on survival rates and lamb:female and yearling:female ratios. However, due to the climatic conditions during the study we were unable to assess how the treatment population would have responded to a lack of water sources during a drought period. The influence of anthropogenic water catchments, if any, on desert bighorn sheep populations may be strongest during years with weather conditions that are neither drought nor wet periods. Given the high interannual variability in precipitation in many areas of the arid Southwest, it is important for wildlife managers to determine if and when water is the primary limiting factor for populations of desert bighorn sheep in order to make the most efficient use of agency time and resources. (WILDLIFE MONOGRAPHS 171:1–30)

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Respuesta del Borrego Cimarrón del Desierto a la Remoción de las Fuentes de Agua

RESEMEN En regiones áridas del suroeste de Estados Unidos, agua es a menudo considerada el primer factor limitante en la distribución y productividad de ungulados, incluyendo el borrego cimarrón del desierto (*Ovis canadensis mexicana)*. Por lo tanto, las agencias de manejo de vida silvestre y organizaciones de deportes han invertido mucho tiempo y recursos en la construcción y mantenimiento de sistemas de captura de agua. A pesar que la disposición de fuentes de agua libre se cree que influencia muchos aspectos de la ecología del borrego cimarrón del desierto, la eficacia de estas fuentes de agua ha sido cuestionada y no ha sido evaluada experimentalmente. Nosotros usamos un estudio denominado control-de-impacto–antes-y-después diseñado para determinar si la remoción de sistemas de captura de agua generan un cambio en el régimen alimenticio, características de las áreas usadas para el forraje por hembras, y el rango de movimiento local, tasas de movimiento, distancia a los sistemas de captura de agua, mortalidad adulta, productividad, y reclutamiento juvenil en dos rangos de montaña en el Refugio de Vida Silvestre Nacional Cabeza Prieta, Arizona. Durante el periodo de pre-tratamiento (2002–2003) nos aseguramos que los sistemas de captura de agua estuvieran disponibles a todos los borregos cimarrón en ambos rangos montañosos; durante el periodo de pos-tratamiento nosotros vaciamos todos los sistemas de captura de agua en el rango de tratamiento. Nosotros medimos la composición dietética, características forrajeras en el área, 50% y 95% kernel de rango local, tasas de movimiento, y las distancias a los sistemas de agua de captura temporalmente desde el 2002 al 2005. También estimamos la sobrevivencia de los adultos, y la relación de las hembras con una año cumplido del 2002 al 2005. Nosotros predijimos que la remoción de sistemas de captura de agua resultaría en lo siguiente: 1) incrementa el uso de aras de forraje con mas cobertura vegetal, mas protección a las temperaturas, y mayor abundancia de suculentas; 2) incremento en consumo de cactáceas y otras suculentas; 3) un incremento en el rango de movimiento local, tasas de movimiento, distancia al sistemas de captura de agua más cercano; 4) un decrecimiento en la tasa de sobrevivencia adulta, productividad y reclutamiento juvenil. La remoción de los sistemas de captura de agua en el rango de tratamiento no resulto en la predicción de cambios de composición dietética, selección de áreas de forraje, tamaño del rango local, tasas de movimiento, mortalidad, productividad o reclutamiento. La hembras de borregos cimarrón usaron áreas de mayor cobertura sombreada durante los meses del verano después de remover los sistemas de captura de agua, pero otras características de áreas de forraje usadas por los borregos cimarrones y su dieta no cambio apreciablemente con la remoción de estos sistemas. No documentamos cambios en el incremento del tamaño del rango de movimiento local, tasas de movimiento, o distancia convencional donde se encuentra agua en meses de verano; cambios en el rango local, tasas de movimiento, y distancias a los sistemas de captura de agua fueron documentados solo durante las temporadas de otoño e invierno. Se encontraron 10 mortalidades de borrego cimarrón en el rango de tratamiento y 8 en el rango control; 7 mortalidades en cada rango montañoso donde durante el periodo de pre-tratamiento. Doce de dieciocho mortalidades ocurrieron durante el verano. Las tasas de movimiento fueron más bajas durante el periodo de pre-tratamiento que durante el pos-tratamiento en ambos rango de montaña. No documentamos incrementos en mortalidad o cambio en los rango de relación borrego: hembra o hembras que han cumplido un ano después de haber removido los sistemas de captura de agua. El rango del area local y tasas de movimiento declinaron con la precipitación. Las tasas de sobrevivencia anual se incrementaron con el incremento en la precipitación total al ano y la precipitación total del año previo; las tasa de sobrevivencia declinaron con el incremento de la temperatura promedio diaria durante el invierno. Se presentaron varias sequias durante el periodo de pre-tratamiento y las condiciones anormalmente húmedas durante el periodo de post-tratamiento pudo proveer agua adecuada para las hembras del borrego cimarrón. Después de remover las fuentes de agua no observamos cambio en el tamaño del rango local, en las tasas de movimiento, y en la distancia al sistema de captura de agua más cercano durante la temporada caliente y seca; esto sugiere que las condiciones del forraje jugó un rol mas importante en determinar el área de rango local y tasas de movimiento que la presencia de sistemas de captura de agua. Las tasas de mortalidad más altas durante la sequia del periodo de pre-tratamiento indica que durante las sequias tan severas como la del 2002, la presencia de sistemas de captura de agua no fue suficiente para prevenir la mortalidad del borrego cimarrón y la carencia de forraje de calidad y cantidad fue el principal factor limitante de la población durante este periodo. Condiciones de forraje mejoradas durante el periodo de pos-tratamiento, incremento el contenido de humedad del forraje, y la disposición de fuentes de agua libre que ocurren naturalmente en el rango de tratamiento posiblemente minimizo cualquier impacto relacionado con la remoción de las fuentes de agua en las tasas de sobrevivencia y la relación borrego: hembra y el rango de hembras de un año o mas:hembras. Sin hembra, debido a las condiciones climáticas durante el estudio nos fue difícil evaluar como la población tratada hubiera respondido a la carencia de fuentes de agua durante un periodo de sequia. La influencia de sistemas de captura de agua antropogénicos, si los hay, en la población de borrego cimarrón podría ser mas fuerte durante condiciones mas húmedas que en sequías o en periodos húmedos. Dado la alta variabilidad interannual en la precipitación en muchas áreas del sudoeste árido, es importante que los encargados de la fauna se determinen si y cuando el agua es el factor limitador primario para las poblaciones de borrego cimarrón del desierto para hacer el uso más eficiente de tiempo y de recursos de la agencia.

Réponses des Mouflon d'Amérique du Désert a la Suppression des Bassins d'Eau

RÉSUMÉ Dans les régions arides du sud-ouest des États-Unis, l'eau est souvent considérée comme un facteur primaire limitant la distribution et la productivité des ongulés du désert, y compris les mouflons d'Amérique du désert (*Ovis canadensis mexicana*). Ainsi, les agences de gestion de la faune et les organisations sportives ont investi beaucoup de temps et de ressources dans la construction et la maintenance de bassins de captage d'eau. Bien que l'accessibilité à des sources d'eau naturelles soit considérée influencer plusieurs aspects de l'écologie du mouflon d'Amérique du désert, l'efficacité de ces sources d'eau a été mise en question et n'a pas été examinée expérimentalement. Nous utilisons un principe d'étude BACI (before-after–control-impact: contrôle des impacts par comparaison avec l'état initial) pour déterminer si la suppression des bassins d'eau change l'alimentation, les caractéristiques des régions de quête alimentaire utilisées par les mouflons d'Amérique du désert femelles, la dimension du domaine vital, les taux de mouvement, la distance jusqu'aux bassins, la mortalité des adultes, la productivité, ou le recrutement des jeunes dans 2 chaînes de montagnes du Cabeza Prieta National Wildlife Refuge en Arizona. Durant la période de prétraitement (2002–2003), nous nous sommes assuré que les bassins de captage d'eau soient disponibles aux mouflons d'Amérique du désert dans les deux chaînes de montagnes ; durant la période de post-traitement (2004–2005), nous avons drainé tous les bassins d'eau dans la zone de traitement. Nous avons mesuré la composition alimentaire, les caractéristiques des régions de quête alimentaire, les 50% et 95% du centre de l'aire vitale, les taux de mouvement, et la distance jusqu'aux bassins de captage d'une façon saisonnière entre 2002 et 2005. Nous avons aussi estimé la survie des adultes, et les rapports agneau:femelle et animaux de 1 an:femelle entre 2002 et 2005. Nous avons prédit que la suppression des bassins de captage d'eau résulterait en: 1) une utilisation plus prononcée des régions de quête alimentaire contenant plus de couverture végétale, plus de couverture thermique, et présentant une abondance de plantes grasses (succulentes) plus élevée; 2) une consommation plus élevée de cactus et autres succulentes; 3) une augmentation de la taille du domaine vital, des taux de mouvement, de la distance jusqu'au bassin le plus proche; 4) une diminution de la survie des adultes, de la productivité et du recrutement des jeunes. La suppression des bassins de captage d'eau dans la zone de traitement n'a pas engendré les modifications prédites en ce qui concerne l'alimentation, la sélection de la région de recherche alimentaire, la taille de l'aire vitale, les taux de mouvement, la mortalité, la productivité ou le recrutement. Les mouflons d'Amérique du désert femelles ont utilisé des régions avec une couverture thermique plus importante durant les mois d'été après la suppression des bassins d'eau, mais les autres caractéristiques liées aux régions de quête alimentaire utilisées par les mouflons d'Amérique du désert ainsi que leur alimentation n'ont pas changé d'une façon remarquable suite à la suppression des bassins de captage. Nous n'avons pas observé de changements liés à la taille de l'aire vitale, aux taux de mouvement, ou à la distance des mouflons aux points d'eau durant

les mois les plus chauds ; nous avons seulement observés des changements liés à la taille de l'aire vitale, aux taux de mouvement, et à la distance jusqu'aux bassins de captage durant les saisons d'hiver et d'automne. Il y a eu 10 mortalités du mouflons d'Amérique dans la zone de traitement et 8 dans la zone de contrôle; il y a eu 7 mortalités dans chaque chaîne de montagne durant la période de prétraitement. Douze des 18 mortalités totales se sont produites durant l'été. Dans les deux chaînes montagneuses, le taux de survie était plus bas durant le prétraitement en comparaison avec la période de post-traitement. Nous n'avons pas observé une augmentation de la mortalité ou un changement dans les rapports agneau:femelle et animaux de 1 an:femelle après la suppression des bassins de captage d'eau. L'aire du domaine vital et les taux de mouvement ont diminué avec l'augmentation des précipitations. Les taux de survie annuels ont augmenté avec l'augmentation des précipitations totales de l'année en cours ainsi que les précipitations totales de l'année précédente; les taux de survie annuels ont diminué avec les augmentations de la température journalière moyenne durant l'hiver. Il y a eu une sécheresse prononcée durant la période de prétraitement ainsi que des conditions inhabituellement humides durant la période de post-traitement. L'augmentation des précipitations qui a coïncidé avec la suppression des sources d'eau a amélioré les conditions de quête alimentaire durant la période de post-traitement et a peut-être pu fournir une source d'eau adéquate pour les mouflons d'Amérique femelles. L'absence de modification de l'aire vitale, des taux de mouvement, et de la distance au bassin de captage d'eau le plus proche durant les saisons chaudes et sèches après la suppression des sources d'eau suggère que les conditions de recherche alimentaire ont eu une influence plus importante sur l'aire du domaine vital et sur les taux de mouvement que la présence ou l'absence de bassins d'eau. Les taux de mortalité plus élevés durant la sécheresse de la période de prétraitement indiquent que durant des sécheresses aussi graves que celle de 2002, la présence de bassins de captage n'était pas suffisante pour éviter les mortalités du mouflon d'Amérique du désert, et il est probable qu'une diminution de la qualité et de la quantité de la recherche alimentaire soit le facteur limitant principal de la population durant cette période. Il est probable que l'amélioration des conditions de quête alimentaire durant la période de post-traitement, l'augmentation du contenu humide lors de la recherche de nourriture, ainsi que la disponibilité de sources naturelles d'eau libre dans la zone de traitement aient minimisé les impacts de la suppression des bassins d'eau sur les taux de survie et sur les rapports agneau:femelle et animaux de 1 an:femelle. Cependant, à cause des conditions climatiques durant l'étude, il nous était impossible d'estimer de quelle manière la population de traitement aurait répondu à un manque de source d'eau durant une période de sécheresse. Il est possible que l'influence des bassins de captage anthropiques, s'ils sont présents, sur les populations de mouflons d'Amérique du désert soit maximale durant les années présentant des conditions météorologiques n'étant des périodes ni de sécheresse ni humides. Etant donné la variabilité interannual élevée dans la précipitation dans beaucoup de secteurs du sud-ouest aride, il est important que les directeurs de faune déterminent si et quand l'eau est le facteur limiteur primaire aux populations des mouflons d'Amérique du désert afin de faire l'utilisation la plus efficace du temps et des ressources d'agence.

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INTRODUCTION

Water is often considered a primary factor limiting the distribution and productivity of desert ungulates (i.e., desert mule deer [*Odocoileus hemionus eremicus*], Sonoran pronghorn [*Antilocapra americana sonoriensis*], desert bighorn sheep [*Ovis canadensis mexicana*]; Leslie and Douglas 1979, Sánchez-Rojas and Gallina 2000, deVos and Miller 2005) in arid regions of the southwestern United States. When water availability is considered scarce or unreliable, wildlife managers and sportsmen's organizations focus considerable effort developing water sources (i.e., water catchments) for wildlife. In efforts to enhance the distribution and productivity of game species, water sources are built in areas where water is naturally scarce and have been used to mitigate for loss of naturally occurring water sources, habitat loss, and landscape alteration resulting from urban, agricultural, transportation, and industrial development (Krausman and Etchberger 1995, Rosenstock et al. 1999, Krausman et al. 2006).

Development of water sources is one of the primary management tools used by wildlife managers in arid regions. At the end of the last century, 10 of 11 western state wildlife agencies had ongoing water catchment programs including approximately 6,000 catchments, guzzlers, tinajas, developed springs, and wells to provide perennial sources of water for wildlife. Overall, >$1,000,000/year is allocated for this activity in the Southwest (Rosenstock et al. 1999, Krausman et al. 2006). Despite the time and resources allocated to wildlife water catchments, relatively little has been dedicated toward monitoring their influence on wildlife.

Although use of water catchments continues to be a popular management tool among wildlife management agencies in the western United States, the efficacy of water catchments has been

questioned and their use controversial (Broyles and Cutler 1999, Czech and Krausman 1999, Rosenstock et al. 2001). Much of the controversy is due to the lack of experimental studies assessing efficacy of water catchments, conflicting results of observational studies, and ungulate occupancy of areas without perennial water sources (Mendoza 1976, Leslie and Douglas 1979, Krausman and Leopold 1986, Warrick and Krausman 1989, Deblinger and Alldredge 1991). Furthermore, most of the physiological studies on thermoregulation and water balance of desert ungulates have been with African and Middle Eastern species; there have been few physiological studies of ungulates inhabiting North American deserts (Turner 1973, 1979, 1984; Cain et al. 2006). In addition, during the past 2 decades, many desert areas with a long history of water catchment construction and maintenance by wildlife management agencies have been designated as wilderness areas and national monuments (e.g., Arizona Desert Wilderness Act of 1990 [Public Law 101-628], California Desert Protection Act of 1994 [Public Law 103-433]). The presence of anthropogenic water sources within these newly designated wilderness areas has become controversial. Because water has been linked to life-history characteristics of desert bighorn sheep, including diet selection, home-range use, survival, and reproductive success, it is important to document the influence of water catchments on desert bighorn sheep.

The diet of desert bighorn sheep has been studied in Arizona (Seegmiller and Ohmart 1981, Smith and Krausman 1987, Krausman et al. 1989, Morgart 1990, Holt et al. 1992), California (Welles and Welles 1961, Ginnett and Douglas 1982, Cunningham and Ohmart 1986, Bleich et al. 1997), Nevada (Barrett 1964, Yoakum 1964, Brown et al. 1977), New Mexico (Sandoval 1979, Watts 1979, Elenowitz 1983), Texas (Brewer 2001, Fulbright et al. 2001), Utah (King and Workman 1982), USA, and Sonora and Baja California Sur, Mexico (Sanchez 1976, Tarango 2000). Previous diet studies have been largely descriptive and most are of a relatively short duration (i.e., $\leq$2 yr); with a few exceptions (Brown et al. 1977, Krausman et al. 1989, Bleich et al. 1997, Etchberger and Krausman 1998) these studies documented temporal and spatial variation in diet of desert bighorn sheep across the desert Southwest. Diet selection of most populations of desert bighorn sheep is thought to be related to water availability, both preformed in forage and freestanding (e.g., water catchments; Welles and Welles 1961, Krausman et al. 1999). However, there have not been experimental studies to determine the influence of freestanding water sources on diet of desert bighorn sheep.

Resource demands of an animal are linked to movements and home-range size. Animals occupying areas with widely dispersed resources or areas with low resource availability often increase movements to acquire enough resources and hence have larger home ranges than do animals in areas with a higher availability of resources (McNab 1963). Habitat productivity also influences home-range size. Animals in highly productive areas are able to meet their resource needs using smaller areas than those inhabiting less productive areas (Jewell 1966, Harestad and Bunnell 1979). Among ungulates, a relationship between habitat productivity and home-range size has been observed in wood bison (*Bos bison athabascae*; Larter and Gates 1994), wild boar (*Sus scrofa*; Singer et al. 1981), roe deer (*Capreolus capreolus*; Tufto et al. 1996, Saïd and Servanty 2005), white-tailed deer (*Odocoileus virginianus*; Beier and McCullough 1990), desert mule deer (Relyea et al. 2000), and desert bighorn sheep (Leslie and Douglas 1979, Krausman et al. 1989, Oehler et al. 2003). Home-range sizes tend to be smaller during times of resource abundance and larger when resources were more limited.

Abundance of forage is often a critical determinant of home-range size in ungulates. In the desert Southwest, availability of free water is thought to be one of the primary factors that influences distribution and productivity of desert ungulates (Wilson 1971, Leslie and Douglas 1979, Turner and Weaver 1980, Sánchez-Rojas and Gallina 2000). Perennial sources of water have been described as a critical habitat component of desert bighorn sheep and a key determinant of habitat quality. As a result, availability of perennial water sources and distance of water from escape terrain (i.e., areas >60% slope) are key components in habitat assessment models for desert bighorn sheep (Ferrier and Bradley 1970, Cunningham 1989, Wakeling and Miller 1990*b*, McCarty and Bailey 1994, Douglas and Leslie 1999).

Water catchments influence distribution of desert bighorn sheep during the hottest and driest times of the year (Wilson 1971, Leslie and Douglas 1979, Bates and Workman 1983, Wakeling and Miller 1990*a*, Alvarez-Cárdenas et al. 2001). Many of these observational studies have found that during summer, desert bighorn sheep are limited in their distribution to areas <4 km from water sources. This relationship is particularly strong among females that likely have higher seasonal water demands due to gestation and lactation (Degen 1977, More and Sahni 1978, Hassan et al. 1988). Therefore, if sources of perennial water are key components of habitat of desert bighorn sheep, a change in the presence of perennial water sources should influence distribution and movements of female desert bighorn sheep.

Although wildlife managers have assumed that water is the primary limiting factor for desert ungulates (Wilson 1971, Leslie and Douglas 1979, Turner and Weaver 1980), there have been few attempts to experimentally examine how water catchments influence desert ungulates (Hervert and Krausman 1986, Krausman and Etchberger 1995, Marshal et al. 2006). Our objectives were to determine 1) seasonal and annual variation in diet composition and vegetation characteristics (e.g., % cover, cacti abundance) in areas where desert bighorn sheep forage; 2) seasonal and annual variation in moisture content of key forage species; 3) effects of removal of water from catchments on diet and selection of foraging areas by desert bighorn sheep; 4) seasonal and annual variation in home-range sizes, movements, and distribution of female desert bighorn sheep relative to water catchments; 5) the effect of removal of water catchments on home-range sizes, movements, and distribution; 6) the effect of removal of catchments on adult survival, productivity, and juvenile recruitment of desert bighorn sheep; and 7) the relationship between seasonal precipitation and home-range size, movements, and distribution of desert bighorn sheep.

We predicted that removal of catchments would result in increased use of foraging areas with more vegetation cover, more thermal cover, and higher succulent abundance between pretreatment and posttreatment, that there would be an increase in

consumption of cacti and other succulents, and that bighorn sheep would select plants to maximize intake of preformed water. We also predicted that removal of water from catchments would result in increases in home-range size, movements, and distance to nearest catchment, as well as decreases in adult survival, productivity, and juvenile recruitment. In addition, we predicted that home-range size and movements would decrease with increases in precipitation and that distance to the nearest catchment would increase with increasing precipitation.

STUDY AREA

We conducted the study on the Cabeza Prieta National Wildlife Refuge (CPNWR) in southwestern Arizona (Fig. 1). The CPNWR encompassed 348,034 ha in Pima and Yuma counties. Most (325,143 ha) of the CPNWR was congressionally designated wilderness (Public Law 101-628). Topography consisted of a series of rugged mountain ranges surrounded by large bajadas and separated by wide alluvial valleys; elevations ranged from 200 m to 900 m.

The study sites were the Sierra Pinta and Cabeza Prieta Mountains, which were jagged, sharply crested, and dissected by steep, rugged canyons; slopes >56° were common. There were 3 water catchments in the Sierra Pinta and 4 in the Cabeza Prieta Mountains (Fig. 2). Ephemerally flowing desert washes and tinajas (temporarily water-filled, natural rock depressions) were also present. However, catchments provided the only known perennial sources of water.

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, AZ, approx. 64 km N of study area) was 10.7 cm. During summer, temperatures were often >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.

Vegetation was typical of the Lower Colorado River Valley subdivision of Sonoran desertscrub. Vegetation in the valleys was characterized by plains of creosote bush (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), and ocotillo (*Fouquieria splendens*). Ironwood (*Olneya tesota*), blue palo verde (*Parkinsonia florida*), and triangle-leafed bursage (*Ambrosia deltoidea*) were common along washes. Vegetation in the 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*), Wright's buckwheat (*Eriogonum wrightii*), 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*), scorpionweed (*Phacelia ambigua*), spiderling (*Boerhavia* spp.), and lupine (*Lupinus* spp.; Simmons 1966, Turner and Brown 1994). Common cacti included giant saguaro (*Cereus giganteus*), barrel cactus (*Ferocactus* spp.), fishhook cactus (*Mammillaria* spp.), teddy bear cholla (*Cylindropuntia bigelovii*), buckhorn cholla (*Cylindropuntia acanthocarpa*), and chain fruit cholla (*Cylindropuntia fulgida*). Plant nomenclature follows Felger (1998).

Native mammalian predators present on the study area included coyote (*Canis latrans*), bobcat (*Lynx rufus*), mountain lion (*Puma concolor*), kit fox (*Vulpes macrotis*), gray fox (*Urocyon cinereoargenteus*), badger (*Taxidea taxus*), and ringtail (*Bassariscus astutus*). Other ungulates present on the study area included desert mule deer, Sonoran pronghorn, and collared peccary (*Pecari tajacu*).

Activities on the CPNWR included wildlife and wilderness management, border security, and recreation. Military aircraft training flights occurred in the airspace over the refuge. Prior land use on the study area included livestock grazing and mining. Over 93% of the CPNWR was a congressionally designated wilderness area that limited access to much of the study area except to those traveling by foot or on horseback. There were 2 public roads on CPNWR, and roads leading to catchments were closed to the public. As a result of limited access, recreational use was also limited, particularly during hot summer months. However, illegal immigration and drug smuggling has increased since the early 1990s and has resulted in increased law enforcement activity (C. S. McCasland, CPNWR, unpublished data).

METHODS

Weather Data

We placed 4 rain gauges in each mountain range. In the Cabeza Prieta Mountains, we located one rain gauge at each water catchment, and in the Sierra Pinta we located one rain gauge at each water catchment and one at the northernmost end of the mountains. We placed 1–2 cm of mineral oil in each rain gauge to minimize evaporation. Because of spatial variation in precipitation, we estimated annual precipitation by calculating the mean precipitation recorded in all rain gauges. We installed 3 HOBO data loggers (Onset Computer Corporation, Bourne, MA) near water catchments in each mountain range to record hourly ambient temperature and relative humidity. We downloaded data from data loggers and recorded contents of rain gauges monthly. Because we expected seasonal variation in response variables, we designated seasons based on annual temperature and precipitation patterns. We defined 1 January–31 March as winter, 1 April–30 June as early summer, 1 July–30 September as late summer, and 1 October–31 December as autumn.

We obtained the monthly Palmer Drought Severity Index (PDSI; Palmer 1965) and the Palmer Z-Index (PZI) from January 1975 through December 2005 for the southwest region of Arizona (National Climate Data Center 2005). The PDSI incorporates precipitation, temperature, and evaporation and is a measure of long-term hydrological drought (Palmer 1965). The PZI represents departure of monthly precipitation totals from average precipitation and is a measure of short-term drought. To assess drought conditions, we compared monthly PDSI and PZI indices during each year of this study with the 30-year monthly averages.

Study Design and Treatment Groups

During 2001, we captured and radiocollared 3 female desert bighorn sheep in the CPNWR to 1) assess efficacy of Global Positioning System (GPS) collars in our study area, 2) collect pilot data on the movements and home ranges of desert bighorn sheep, and 3) assess logistical constraints associated with working in

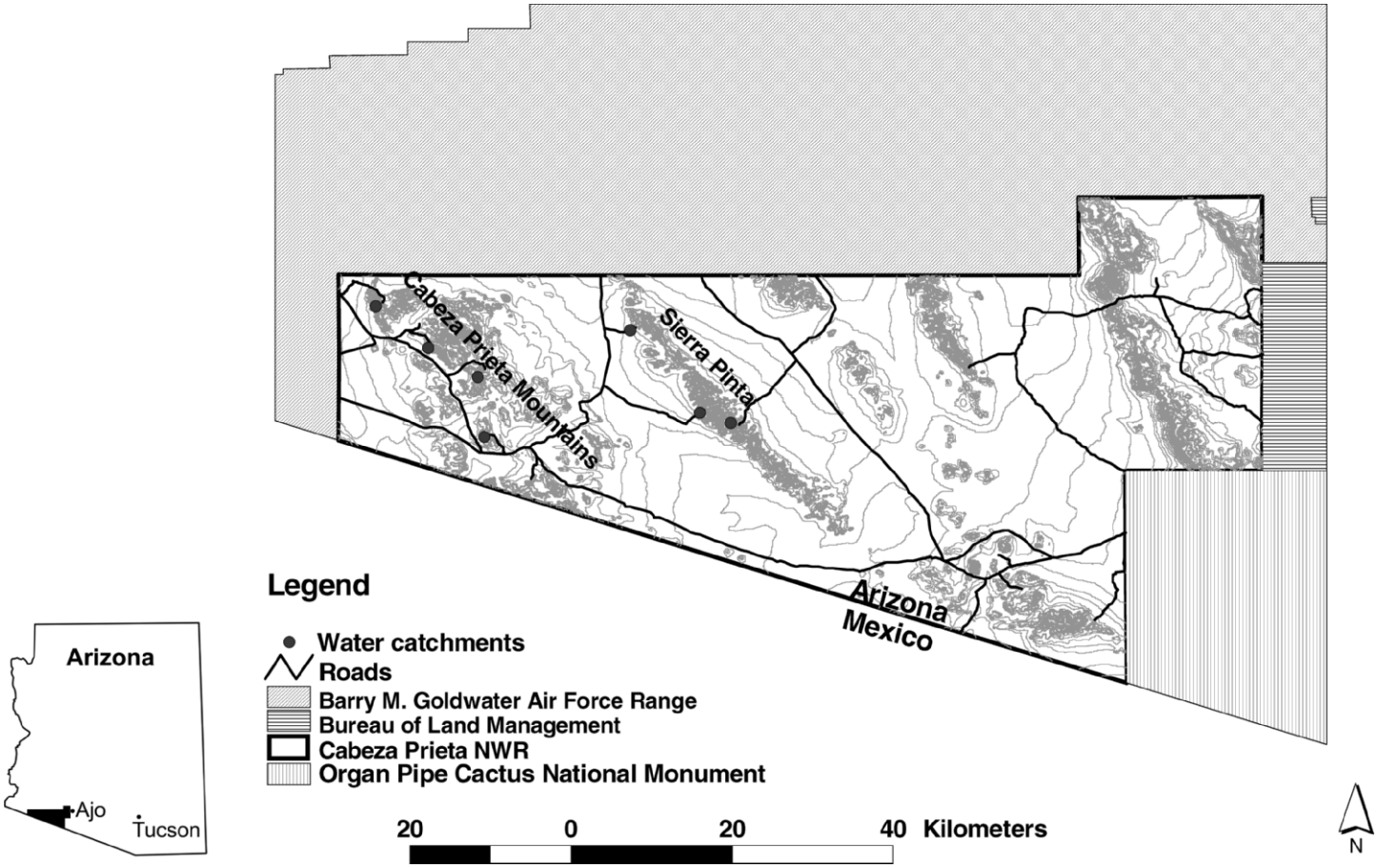

Figure 1. Location of the study area on the Cabeza Prieta National Wildlife Refuge, southwestern Arizona, USA, where the responses of desert bighorn sheep to removal of water sources were investigated, 2002–2005.

different areas of the CPNWR. Based on this data, we determined that to detect a 10% difference in home-range area with 85% power ≥6 radiocollared animals per mountain range would be necessary. Average female population estimates (± SE) were 42.5 ± 3.03 and 30.5 ± 3.01 for the Cabeza Prieta Mountains and Sierra Pinta, respectively (J. W. Cain, University of Arizona, unpublished data).

We used a before-after–control-impact (BACI) design to assess the influence of water catchments on desert bighorn sheep (Stewart-Oaten et al. 1986, 1992). We used the Sierra Pinta as the treatment range and the Cabeza Prieta Mountains as the control range (hereafter treatment and control ranges, respectively). During the first 2 years of the study (pretreatment: Feb 2002–Feb 2004), we checked water catchments in both mountain ranges monthly to ensure they all contained water for desert bighorn sheep. When water levels declined, United States Fish and Wildlife Service and Arizona Game and Fish Department personnel hauled water to the catchments with trucks or helicopters.

On 1 March 2004, we drained all 3 water catchments in the treatment range. We installed 2 float-switch–activated, submersible utility pumps (model FPOS4100X; Flotec, Delavan, WI) in each catchment. We connected 8 6-V deep-cycle lead-acid marine batteries in series to make 24-V battery banks to power the pump systems. We charged the battery bank using a 185-watt solar panel (model NT185U1; Sharp Electronics Corp., Mahwah, NJ). Additional details describing pump systems are available in Cain (2006). We used the pump systems to keep catchments drained from 1 March 2004 until 21 October 2005 (Fig. 3).

Animal Capture and Monitoring

We captured 37 adult female bighorn sheep with a net gun fired from a helicopter (Krausman et al. 1985) and maintained 6–10 radiocollared animals in each mountain range throughout the study. In February 2002, we captured 6 adult females from each mountain range. Subsequent captures were to replace animals lost to mortality, replace radiocollars at the end of battery life, and augment our sample of study animals. We focused our capture efforts on adult females of prime breeding age (4–6 yr old). We aged animals using tooth replacement pattern and horn-ring characteristics (Geist 1966, Hansen and Deming 1980). We followed acceptable methods for capture and handling of study animals (Animal Care and Use Committee 1998, University of Arizona Animal Care and Use Protocols 01-191 and 04-180).

We placed GPS telemetry collars (900 g; models 440 and 3580, Telonics, Mesa, AZ) programmed to record one location every 13 hours on captured animals. Each collar was equipped with a very-high-frequency beacon, a satellite transmitter (platform transmitter terminal). All location data were stored in the GPS collars. In addition, we used the satellite transmitter in conjunction with the

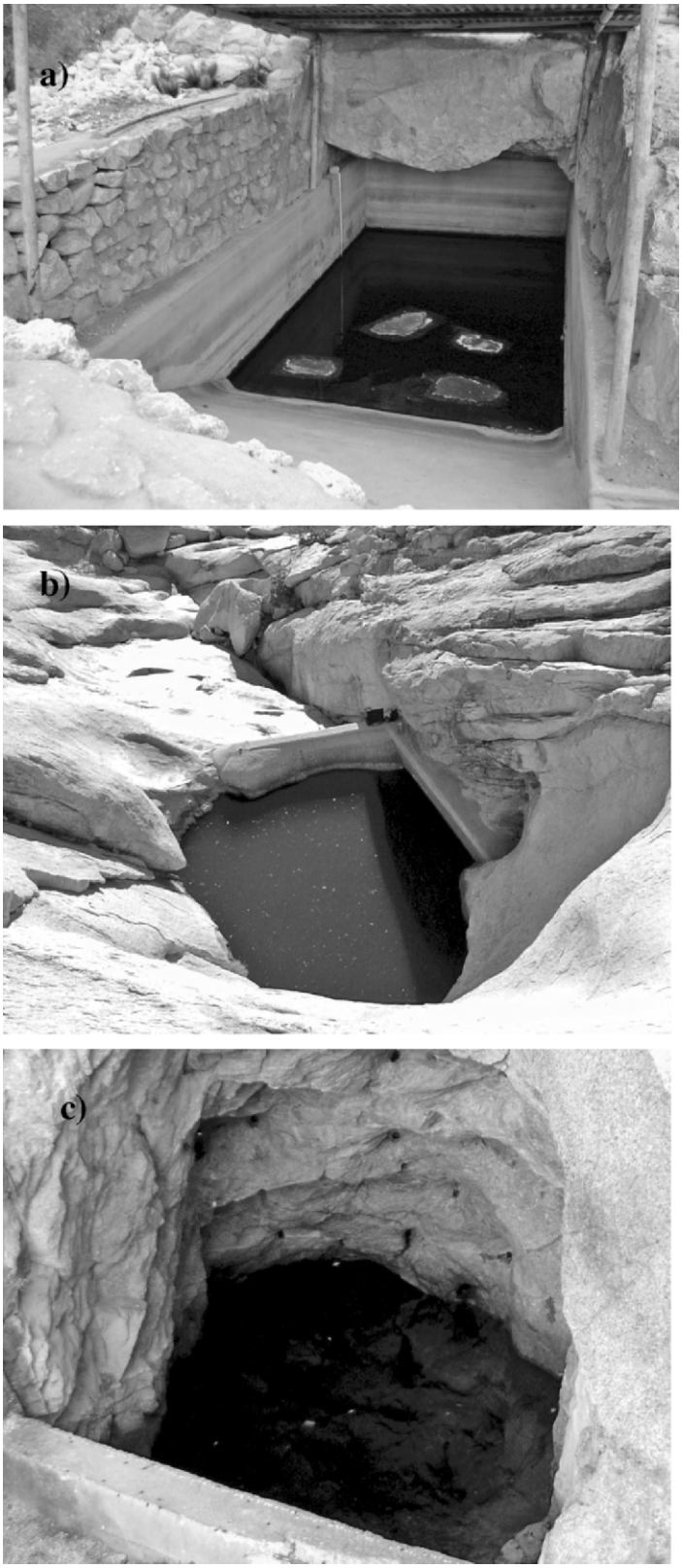

Figure 2. Types of water catchments for desert bighorn sheep during 2001–2005 in the Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona, USA, include (a) concrete box tanks, (b) modified tinajas, and (c) adits.

Argos (Service Argos, Largo, MD) satellite system to transmit GPS location data every 3 days.

Diet Analysis

To estimate diet and determine effects of catchment closures on diet composition, we collected 10–20 pellet groups per season per mountain range from female desert bighorn sheep for microhistological analysis. We collected pellets from radiocollared sheep and uncollared adult female sheep that were either associated with radiocollared animals or opportunistically observed. We analyzed 3 slides per pellet group and sampled 20 randomly selected microscope fields per slide (Sparks and Malechek 1968, Holechek and Vavra 1981, Krausman et al. 1989). We identified plant species using characteristics of the epidermis and cuticle. We determined frequency, particle density, and percent composition for each species (Fracker and Brischle 1944, Sparks and Malechek 1968). We classified plant species as forb (i.e., annual herbaceous vegetation), browse (i.e., perennial woody plants), grass, and succulent (i.e., cacti and agave; Krausman et al. 1989). Although we recognize potential problems associated with differential digestibility of some plant species, we assumed potential biases would equally affect estimates of diet composition for both mountain ranges and across treatment periods (Fitzgerald and Waddington 1979, Holechek et al. 1982, Gill et al. 1983).

We compared similarity of seasonal diets between treatment and control ranges using the Morisita–Horn index (Morisita 1959, Horn 1966, Zaret and Rand 1971, Alcoze and Zimmerman 1973), which is the similarity index least affected by sample size and species richness and incorporates the number of species and relative proportions of each plant species in the diet (Wolda 1981, Magurran 2004). The Morisita–Horn index ranges from zero to one, with values >0.6 indicating substantial overlap in diet and a value of 1 indicating a complete overlap of diet. We used Program EstimateS 7.5 to calculate Morisita–Horn similarity coefficients for percent composition (Colwell 2005).

Foraging Area Characteristics

We used GPS positions obtained from telemetry collars to establish sampling locations to estimate plant cover by forage class (i.e., browse, grass, forbs), thermal cover abundance, succulent abundance, and forage moisture content for each foraging area location. We used GPS positions obtained during specific daily time periods when desert bighorn sheep were most likely to be foraging (0600–0800 hr, 1200–1400 hr, 1600–2000 hr in early summer; 0600–0800 hr, 1500–2000 hr in late summer; 0500–0900 hr, 1400 hr–dusk in autumn; and 0600–0800 hr, 1600–2000 hr in winter; Chilelli and Krausman 1981, Alderman et al. 1989). Because of seasonal variation in timing of feeding periods, we used GPS positions that corresponded to the different seasonal feeding periods to establish vegetation sampling locations. We used the GPS position to determine the center point of each plot. We sampled 8–10 forage plots per range per season. We randomly selected 8–10 animals and chose the most recent location recorded in the appropriate time period. If the most recent GPS position was recorded >2 days prior to selection, we randomly selected another animal and GPS location. We sampled all plots within a

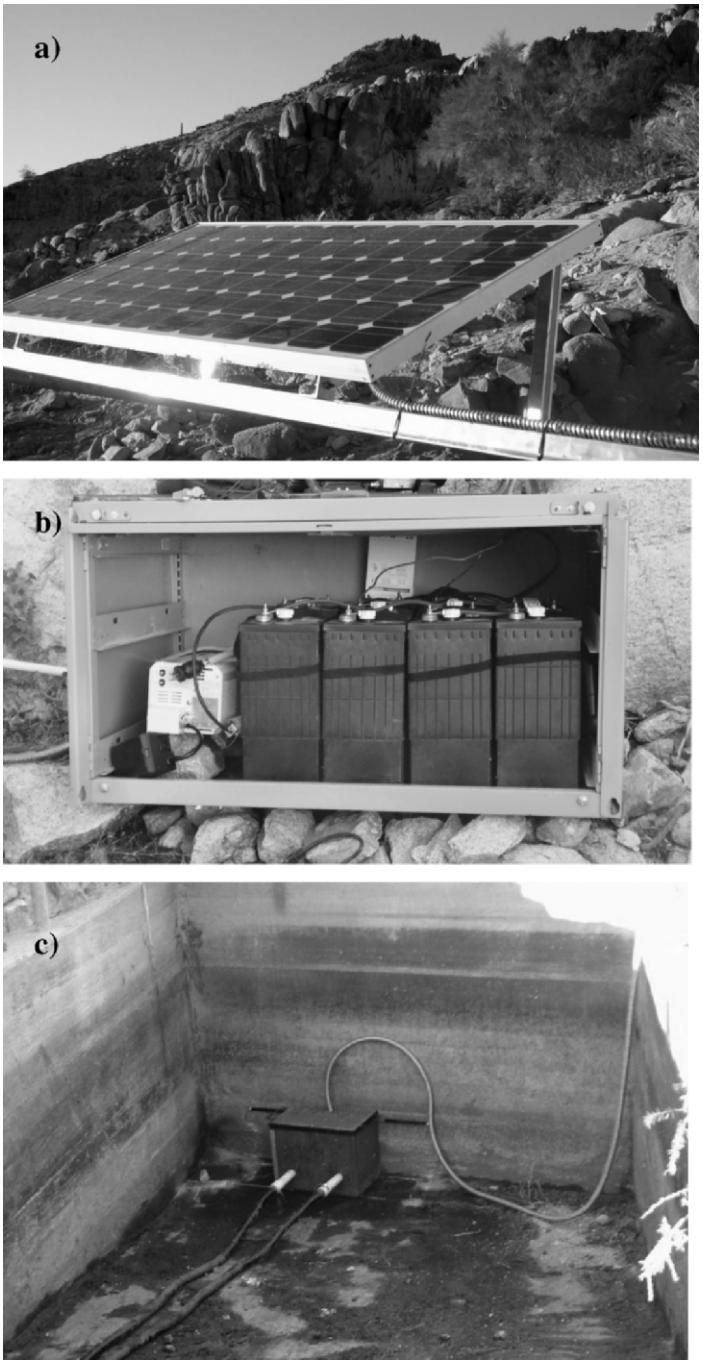

Figure 3. Pump systems used to drain water catchments for desert bighorn sheep during posttreatment (2004–2005) in the Sierra Pinta, southwestern Arizona, USA, were composed of (a) 185-watt solar panel, (b) battery bank with inverter and load controller, and (c) submersible utility pumps housed in filter box.

season during a 4-day to 5-day period during the middle of each season (i.e., in Feb, May, Aug, and Nov).

To determine percent cover and composition of different plant species in the foraging areas, we used a modified version of the line-intercept method (Canfield 1941, Etchberger and Krausman 1997). We established 4 30-m line transects radiating outward from the center point of each plot. We based the direction of the first transect on a randomly selected compass bearing and located the remaining 3 transects at 90°, 180°, and 270° from the first transect, which effectively created a 60 × 60-m square plot. We then measured all vegetation to the nearest 1 cm that intercepted each line transect. We estimated percent cover for each plant species by dividing the accumulated length of the all transects covered by each species by the total length of all line transects (i.e., we pooled data from all 4 transects in a plot; Canfield 1941, Etchberger and Krausman 1997). We then pooled cover estimates for all species into 3 categories: browse, grass, and forbs. We measured abundance of thermal cover by counting the number of plants >1.5 m in height that could provide shade for desert bighorn sheep that intercepted the line transects. We measured abundance of succulents by counting all individual cacti and agave located within the 60 × 60-m plot area, with the exception of fishhook mammillaria cacti, which we excluded because their small size and cryptic nature prohibited accurate counts.

To determine seasonal and annual variation in plant moisture content, we collected forage species for water-content analysis. We collected ≥100 g of each plant species important in the diet of desert bighorn sheep in Arizona (Simmons 1969, Browning and Monson 1980, Morgart et al. 1986, Krausman et al. 1989) from each 60 × 60-m forage plot. We collected the 6 most common grass, 6 most common forb, 6 most common browse species, and 3 species of succulents from each foraging area we sampled, based on visual estimation of within-plot plant abundance and known use by bighorn sheep. All samples were composites of >4 individual plants, unless there were <4 individuals in the plot. We weighed plant samples immediately postcollection to determine fresh weight. We dried plant samples at 50° C in a drying oven (Model 320; National Appliance Company, Portland, OR) to a constant weight, determined dry weight, and calculated percent moisture (Alderman et al. 1989, Fox 1997).

Home Range, Movement Rate, and Distance to Water Catchments

Home range.—Home-range area is commonly presented in terms of planimetric or map area (Jenness 2004*a*); however, areas inhabited by desert bighorn sheep are extremely rugged with a high degree of topographic relief (McCarty and Bailey 1994, Andrew et al. 1999, Krausman et al. 1999, Alvarez-Cárdenas et al. 2001). Given that the amount of resources available for desert bighorn sheep are likely related to surface area, assessments of movements and home-range size of desert bighorn sheep should incorporate actual surface area of the landscape rather than planimetric area. We used the Animal Movements extension for ArcView (Hooge and Eichenlaub 1997, Environmental System Research Institute 2000*a*) to estimate seasonal 95% and 50% fixed-kernel home ranges (Worton 1989, 1995; Seaman and Powell 1996). We selected the smoothing parameter using least-squares cross validation (Worton 1989, Seaman and Powell 1996, Seaman et al. 1999).

To model the surface of our study area, we used United States Geological Survey 1:24,000 digital elevation models (DEMs) with 10 × 10-m cells. We used the Spatial Analyst extension for ArcView to join all DEMs to form one seamless 10 × 10-m DEM of our study area (Environmental System Research Institute 2000*a*, *b*). We then calculated the surface area (km^2) of all kernel home ranges using the Surface Areas and Ratios extension for

ArcView (Jenness 2002, 2004*a*) and calculated the mean 95% and 50% kernel home ranges for each season and mountain range.

Movement rate.—Home ranges are one measure of an animal's activity (Boulanger and White 1990). Seasonal changes in resources can influence how far an animal needs to travel to meet its daily requirements of food and water. To assess seasonal movements of desert bighorn sheep prior to and after removal of anthropogenic water sources, we created a polyline shapefile in ArcView 3.2, connecting all consecutive locations for each animal with a straight line using the Animal Movements extension for ArcView (Hooge and Eichenlaub 1997, Environmental System Research Institute 2000*a*). We used the Surface Tools for Points, Lines, and Polygons extension for ArcView (Jenness 2005) and the seamless 10 × 10-m DEM of our study area to calculate the surface distance between consecutive locations.

Habitat characteristics (i.e., topography, vegetation) and animal behavior can interfere with signal transmission between GPS satellites and receivers, affecting fix success rates of collars (Rempel et al. 1995, Moen et al. 2001, D'Eon et al. 2002, Cain et al. 2005). To account for missing GPS locations, we converted our movement distances to movement rates (m/hr) by dividing the surface distance between each pair of consecutive GPS locations by the number of elapsed hours between locations. For each individual animal, we calculated the average movement rate for each season and year. For each mountain range, we then calculated an overall seasonal movement rate by taking the mean of seasonal movement rates of individual animals.

Distance to water catchments.—To determine if distribution of desert bighorn sheep was associated with anthropogenic water sources and if removal of these water sources influenced the distribution of desert bighorn sheep, we used the Nearest Features, with Distances and Bearings extension for ArcView to connect each GPS location and the nearest anthropogenic water source with a straight line (Jenness 2004*b*). We then used the Surface Tools for Points, Lines, and Polygons extension for ArcView (Jenness 2005) and the seamless 10 × 10-m DEM of our study area to calculate the surface distance between each location and the nearest anthropogenic water source. For each animal, we calculated mean distance to the nearest water source for each season and year. Then, for each mountain range, we calculated overall seasonal distance to the nearest water source by taking the mean of the seasonal distance to the nearest water source of the individual animals.

Adult Survival, Productivity, and Recruitment

Adult survival.—We used the known-fates model in Program MARK 4.2 to estimate total and annual survival rates and standard errors for each mountain range (White and Burnham 1999). In addition, to compare survival during hot versus cool seasons, we combined all seasons into 4 hot (early and late summer 2002, early and late summer 2003, early and late summer 2004, and early and late summer 2005) and 4 cool seasons (winter 2002, autumn 2002 and winter 2003, autumn 2003 and winter 2004, and autumn 2004 and winter 2005) for each mountain range.

Productivity and recruitment.—To assess productivity and recruitment, we surveyed all areas of each mountain range annually, recording age, sex, and group size of all animals observed. We surveyed each mountain range in mid-October to early November each year using a helicopter (Bell 206B JetRanger and Bell 206L LongRanger; Bell Helicopter Textron, Inc., Fort Worth, TX) and attempted to standardize factors that may influence survey results. We flew all surveys at the same time of day and at constant survey intensity of 2.9 minutes/km^2 (Hervert et al. 1998). We flew all surveys with 3 observers: one observer on each side of the helicopter in the rear seats and one observer in the front left seat. The pilot was in the front right seat and was not an observer. We used the simultaneous double-count method to estimate detectability of desert bighorn sheep using observations by the front and rear left-side observers (Graham and Bell 1989, Hervert et al. 1998). We calculated the sighting probability and variance for the front observer only, the rear observer only, and the probability that an animal will be observed by $\geq$1 left-side observer following Skalski et al. (2005). Because there was only one observer on the right side of the helicopter, we applied the calculated probability and variance estimate of an animal or group being observed by the left-rear observer only to the right-rear observer. We calculated sighting probabilities for single animals and groups of $\geq$2 animals for each survey in each mountain range. We then used the calculated sighting probabilities and their associated variance estimates to estimate the yearling:female and lamb:female ratios in each mountain range (Samuel et al. 1992, Skalski et al. 2005).

Statistical Analysis

Prior to analysis, we examined all data for normality and homogeneity of variances. We used arcsine square-root, square-root, and log transformation when data failed to meet parametric assumptions (Zar 1996). We present means and standard errors in the original scale of measurement. We set α at 0.10 for all analyses to increase statistical power and reduce probability of committing a Type II error. We performed all statistical analyses using SPSS 10.0.7 (SPSS, Chicago, IL).

To determine if removal of water catchments influenced diet, foraging area characteristics (e.g., % cover by forage class), home-range size, movement, distance to water catchments, annual survival, seasonal (i.e., hot vs. cool season) survival, lamb:female ratios, and yearling:female ratios, we used the 2-factor analysis of variance (ANOVA) described by Underwood (1994) for detection of environmental impact with a BACI study. We used mountain range and treatment period as fixed factors. A significant mountain range × treatment period interaction term indicates that the magnitude of the difference from pre- to posttreatment changed in the treatment mountain range relative to the control range (Underwood 1994). We used all seasons (i.e., early summer 2002 to late summer 2005) from pretreatment and posttreatment as replicates. We also analyzed individual seasons (i.e., winter, early summer, late summer, and autumn) using the pretreatment and posttreatment years as independent samples.

We used 2-factor ANOVA, with season and treatment period as fixed factors to determine if the degree of dietary overlap (i.e., % composition) changed in response to removal of water sources in the treatment range. We grouped all plant species collected for moisture content analysis into their respective forage classes, then calculated mean moisture content for each forage class during each season (early summer 2002 to late summer 2005) for each mountain range. We used ANOVA to determine if the mean moisture content of the 4 forage classes differed between seasons,

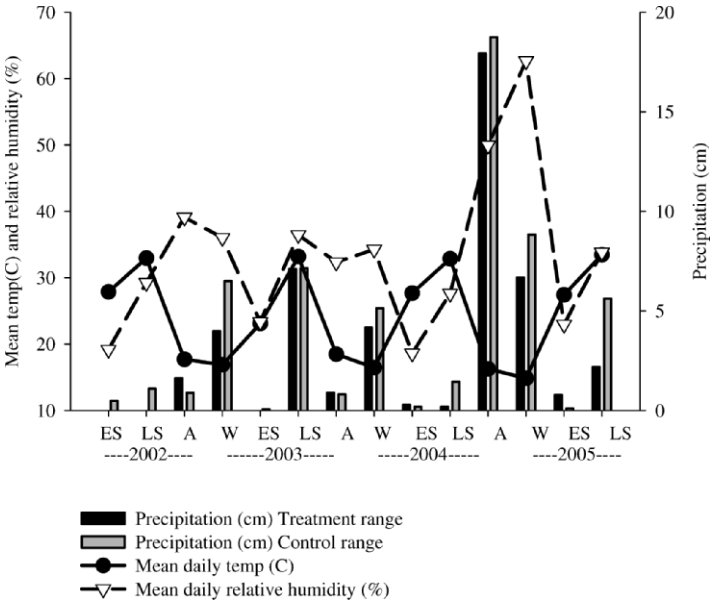

Figure 4. Seasonal mean daily temperature (° C), relative humidity (%), and precipitation totals (cm) for the Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona, USA, early summer (ES) 2002 to late summer (LS) 2005; W = winter, A = autumn.

mountain ranges, or years. We used linear regression to determine if home-range area, movement rates, distance to nearest catchment, survival rates, and lamb:female and yearling:female ratios were associated with annual, seasonal, and monthly precipitation patterns.

RESULTS

Weather Data

Mean annual precipitation (± SD) during the study was 3.5 ± 1.88 cm, 13.3 ± 3.09 cm, 24.1 ± 2.88 cm, and 12.1 ± 3.02 cm during 2002, 2003, 2004, and 2005, respectively (Fig. 4). Seasonal mean daily temperatures (± SD) were 16.1 ± 6.45° C, 26.9 ± 8.55° C, 33.1 ± 6.57° C, and 17.4 ± 7.83° C for winter, early summer, late summer, and autumn, respectively. Seasonal mean daily temperatures were an average (± SE) of 1.8 ± 0.04° C, 1.9 ± 0.18° C, 1.5 ± 0.22° C, and 2.4 ± 0.42° C higher in the treatment range than in the control range during winter (range = 0.8–2.4° C), early summer (range = 1.6–2.4° C), late summer (range = 1.1–2.0° C), and autumn (range = 1.9–3.2° C), respectively. Seasonal mean daily relative humidity (± SE) was 3.1 ± 2.04%, 1.8 ± 1.09%, and 1.3 ± 1.32% lower in the treatment range than in the control range during winter (range = 0–8.8%), early summer (range = 0–3.7%), and late summer (range = 0–4.4%), respectively.

There was a severe drought in southwestern Arizona during pretreatment (2002–2003; Fig. 5a). The monthly PDSI remained <0 from the initiation of this study until September 2004 when increased precipitation resulted in a PDSI >0 (Fig. 5a). Similarly the monthly PZI was ≤0 during 2002 and 2003, increased beginning in September 2004, and remained >0 for the remainder of the study, with the exception of September 2005 (Fig. 5b).

Diet Analysis

Seasonal diet composition was similar between mountain ranges during pretreatment and posttreatment (Table 1). Browse composed most (≥68%) of diets in both mountain ranges during all seasons (Fig. 6). Cacti composed the second highest proportion (range = 9–23%) of the diet in both ranges during all seasons, except for winter and early summer of 2004 and winter 2005 in the control range when forb consumption increased (Fig. 6). The proportion of cacti in the diet was highest during late summer (range = 13.7–21.9%) and winter (range = 7.0–22.6%) in both mountain ranges. Seasonal variation in grass consumption was similar in both mountain ranges, peaking in late summer during pretreatment years and late summer and winter in posttreatment years (Fig. 6). Seasonal forb consumption was also similar between mountain ranges and was highest during winter and early summer in all years.

We found slight evidence for a range × treatment interaction comparing changes in seasonal browse consumption ($F_{1,28}$ = 2.763, P = 0.108), indicating an effect of treatment on browse use. During early summer, browse consumption increased (± SE) by 9.8 ± 0.623% in the treatment range and decreased by 4.9 ± 3.702% in the control range from pretreatment to posttreatment. Browse consumption in the treatment and control ranges during winter, late summer, and autumn were similar from pretreatment to posttreatment (Fig. 6). Differences in the proportion of grass ($F_{1,28}$ = 0.122, P = 0.733), forbs ($F_{1,28}$ = 0.164, P = 0.693), and cacti ($F_{1,28}$ = 1.25, P = 0.286) in the diet did not change in response to the treatment during any season (Table 1).

There were 43 and 42 plant species in the diets of female desert bighorn sheep in the treatment and control ranges, respectively (Tables 2–5). Average number of species found in the diet varied seasonally in both mountain ranges. From 2002 to 2005, we identified an average (± SD) of 27 ± 7.9, 26 ± 2.5, 25 ± 4.9, and 22 ± 1.5 plant species in diets of female bighorn sheep from the treatment range during winter, early summer, late summer, and autumn, respectively, whereas an average of 27 ± 6.7, 26 ± 3.1, 27 ± 3.7, and 21 ± 1.0 species were identified in diets of animals from the control range. Most (>73%) of the diet was composed of silverbush (*Ditaxis lanceolata*), palo verde, ironwood, desert lavender (*Hyptis emoryi*), big galleta grass, Wright's buckwheat, and fishhook mammillaria cacti and cholla. These 7 plants composed an average (± SE) of 73 ± 9.42%, 79 ± 2.7%, 88 ± 3.5%, and 83 ± 4.6% of the diets in the treatment range and 70 ± 9.1%, 66 ± 3.5%, 72 ± 3.2%, and 85 ± 1.3% in the control range during winter, early summer, late summer, and autumn, respectively (Tables 2–5). Other plant species representing ≥3% of the diet during ≥1 season included brittlebush, catclaw acacia, filaree (*Erodium cicutarium*), borage (*Cryptantha* spp.), globe mallow (*Sphaeralcea* spp.), Indian wheat, janusia (*Janusia gracilis*), mesquite (*Prosopis* spp.), ephedra (*Ephedra nevadensis*), and golondrina (*Euphorbia* spp.; Tables 2–5). Morisita–Horn similarity coefficients were >0.90 during all seasons during pre- and posttreatment, indicating substantial overlap in diet of female desert bighorn sheep in the treatment and control ranges (Table 6). Diet overlap between treatment and control ranges did not change in response to treatment ($F_{1,14}$ = 0.485, P = 0.705).

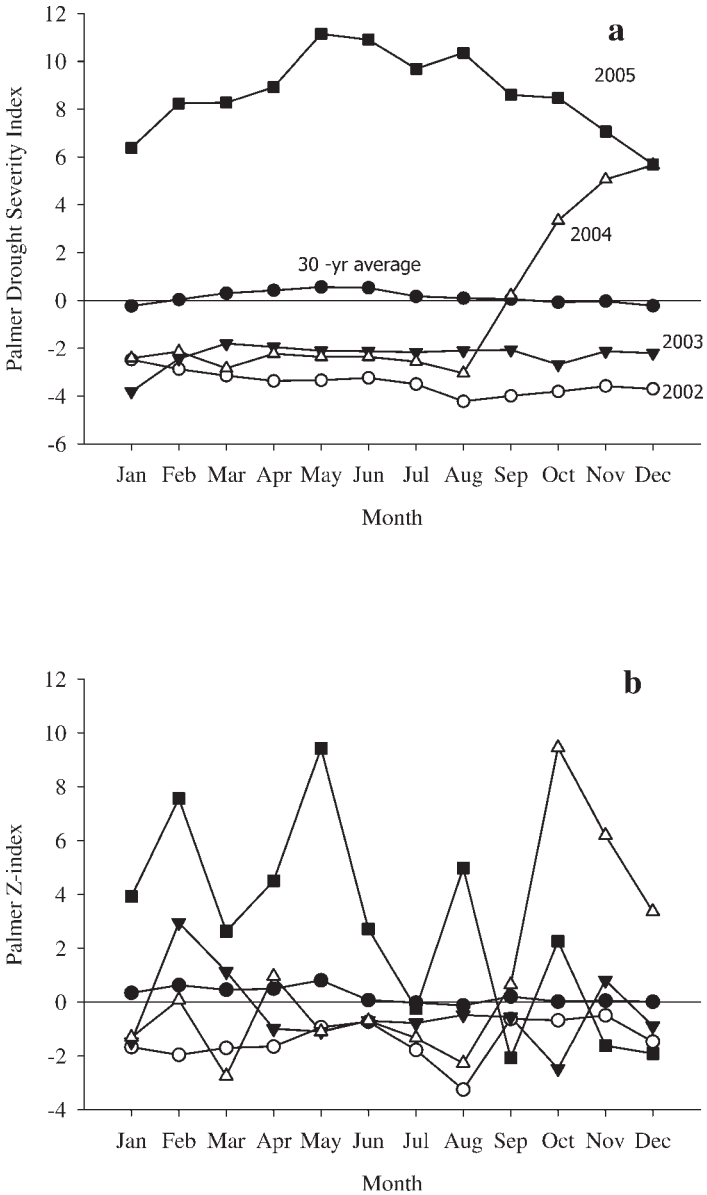

Figure 5. Monthly (a) Palmer Drought Severity Index and (b) Palmer Z-index for southwestern Arizona, USA (negative values indicate drought conditions; positive values indicate wet conditions); 30-year monthly averages and individual years 2002–2005.

Foraging Area Characteristics

Desert bighorn sheep foraging areas had similar cover of browse ($F_{1,28} = 0.003$, $P = 0.954$), forb ($F_{1,28} = 0.001$, $P = 0.972$), grass ($F_{1,28} = 0.698$, $P = 0.423$), and cacti ($F_{1,28} = 0.733$, $P = 0.409$) in the treatment and control ranges from pretreatment to posttreatment (Fig. 7).

Desert bighorn sheep used foraging areas in the treatment range with 69.6% (pretreatment: 2.3 ± 0.38%; posttreatment: 3.9 ± 0.01%) more thermal cover during early summer and 95.5% (pretreatment: 2.2 ± 0.08%; posttreatment: 4.3 ± 0.38%) during late summer from pretreatment to posttreatment ($F_{1,28} = 11.02$, $P = 0.006$). Thermal cover abundance in forage plots was similar from pretreatment to posttreatment during winter and autumn in the treatment range and during all seasons in the control range (Fig. 8).

Abundance of cacti in forage plots varied seasonally in both mountain ranges (Fig. 8). Bighorn sheep in the control range used foraging areas in the late summer with 55.4% less cacti (pretreatment: 21.1 ± 2.33%; posttreatment: 9.4 ± 1.65%) during posttreatment than during pretreatment ($F_{1,28} = 16.75$, $P = 0.006$). Succulent abundance in forage plots was similar from pretreatment to posttreatment during all seasons in the treatment range and during the winter, early summer, and autumn in the control range (Fig. 8).

Moisture content of plants in the 4 forage classes in both the treatment and control ranges varied seasonally and showed an overall increasing trend from pretreatment to posttreatment (Fig. 9). Forbs were only available to be collected during winter 2003–2005 and early summer 2005. Mean moisture content of forbs (± SE) was 0.84 ± 0.06 in the treatment range and 0.81 ± 0.06 in the control range. Overall, moisture content was not different between mountain ranges for all forage classes ($F_{1,83} = 0.659$, $P = 0.420$; $P \geq 0.325$ for all interaction terms that included mountain range). Mean moisture content for all years of the study was 0.45 ± 0.005, 0.27 ± 0.002, 0.82 ± 0.004, and 0.80 ± 0.007 for browse, grass, forbs, and cacti, respectively.

Average seasonal moisture content (± SE) for the 17 plant species that contributed ≥3% to seasonal bighorn sheep diets in the treatment range was 0.52 ± 0.015 for winter, 0.45 ± 0.009 for early summer, 0.41 ± 0.012 for late summer, and 0.54 ± 0.017 for autumn; in the control range average seasonal moisture content of these same species was 0.51 ± 0.016 for winter, 0.46 ± 0.009 for early summer, 0.41 ± 0.012 for late summer, and 0.53 ± 0.016 for autumn in the treatment range. Seasonal moisture content of the 7 key forage species (including fishhook mammillaria and cholla) and cacti (i.e., barrel cactus and agave) indicated that forage with >40% moisture content was available in all seasons (Table 7).

Average moisture content during posttreatment was 79% (range = 77–87%) for desert agave (*Agave deserti*), 92% (range = 89–99%) for barrel cactus, and 75% (range = 65–92%) for fishhook mammillaria. During the drought of the pretreatment years, mean moisture content for these same species was 74% (range = 69–77%), 90% (range = 89–93%), and 65% (range = 61–71%) for desert agave, barrel cactus, and fishhook mammillaria, respectively.

Home Range, Movement Rate, and Distance to Water Catchments

During the study, GPS collars ($n = 43$) from both mountain ranges recorded 23,494 bighorn sheep locations. Collar performance varied between collars, ranging from 55% to 97% fix success rate ($\bar{x} = 72.4\%$; SD = 10.0%).

Home range.—We found evidence for a range × treatment interaction comparing changes in home-range area ($F_{1,28} = 6.14$, $P = 0.019$). Home ranges (95% kernel; ±SE) during winter increased in the treatment range from 12.5 ± 0.95 km^2 to 19.6 ± 1.39 km^2 and decreased from 10.1 ± 3.89 km^2 to 5.2 ± 1.10 km^2 in the control range from pretreatment to posttreatment ($F_{1,6} = 7.85$, $P = 0.031$). During autumn, 95% home range increased from 12.9 ± 1.21 km^2 to 22.1 km^2 in the treatment range and decreased from 11.6 ± 1.24 km^2 to 10.7 km^2 in the control range ($F_{1,6} = 11.02$, $P = 0.016$). We did not find a treatment effect for

Table 1. Percent contribution of grass, browse, succulent, and forb species in the seasonal diet of female desert bighorn sheep in the treatment (Sierra Pinta) and control (Cabeza Prieta) mountain ranges during pre- (2002–2003) and posttreatment (2004–2005), Cabeza Prieta National Wildlife Refuge, Arizona, USA.

		Treatment mountain range				Control mountain range			
		Pretreatment		Posttreatment		Pretreatment		Posttreatment	
Forage class	Season	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Grass	Winter	1.52	[a]	5.18	0.42	1.51	[a]	3.50	1.13
Browse	Winter	75.59	[a]	71.37	1.60	76.70	[a]	72.75	3.56
Succulent	Winter	22.59	[a]	8.92	4.91	17.13	[a]	7.04	4.66
Forb	Winter	0.32	[a]	14.05	3.10	4.66	[a]	16.71	2.23
Grass	Early summer	5.96	1.59	1.37	0.42	4.13	1.95	0.79	0.66
Browse	Early summer	71.05	0.48	80.86	2.23	75.78	1.78	70.85	3.25
Succulent	Early summer	18.67	2.07	10.26	2.76	17.50	2.41	11.55	2.63
Forb	Early summer	4.32	4.13	7.50	2.80	2.58	2.58	16.81	6.54
Grass	Late summer	7.56	1.99	4.18	2.51	8.58	0.07	4.81	2.19
Browse	Late summer	71.09	1.78	73.73	5.23	69.22	0.16	76.37	0.25
Succulent	Late summer	21.26	0.15	14.83	2.42	21.94	0.17	13.76	0.44
Forb	Late summer	0.10	0.05	7.26	5.32	0.26	0.06	5.07	2.38
Grass	Autumn	2.55	0.14	2.95	[b]	3.54	0.85	2.54	[b]
Browse	Autumn	77.47	0.71	84.10	[b]	82.81	1.43	83.63	[b]
Succulent	Autumn	19.90	0.58	9.75	[b]	13.54	0.59	11.82	[b]
Forb	Autumn	0.08	0.01	3.20	[b]	0.11	0.88	2.01	[b]

[a] Only one winter season during pretreatment.
[b] Only one autumn season during posttreatment.

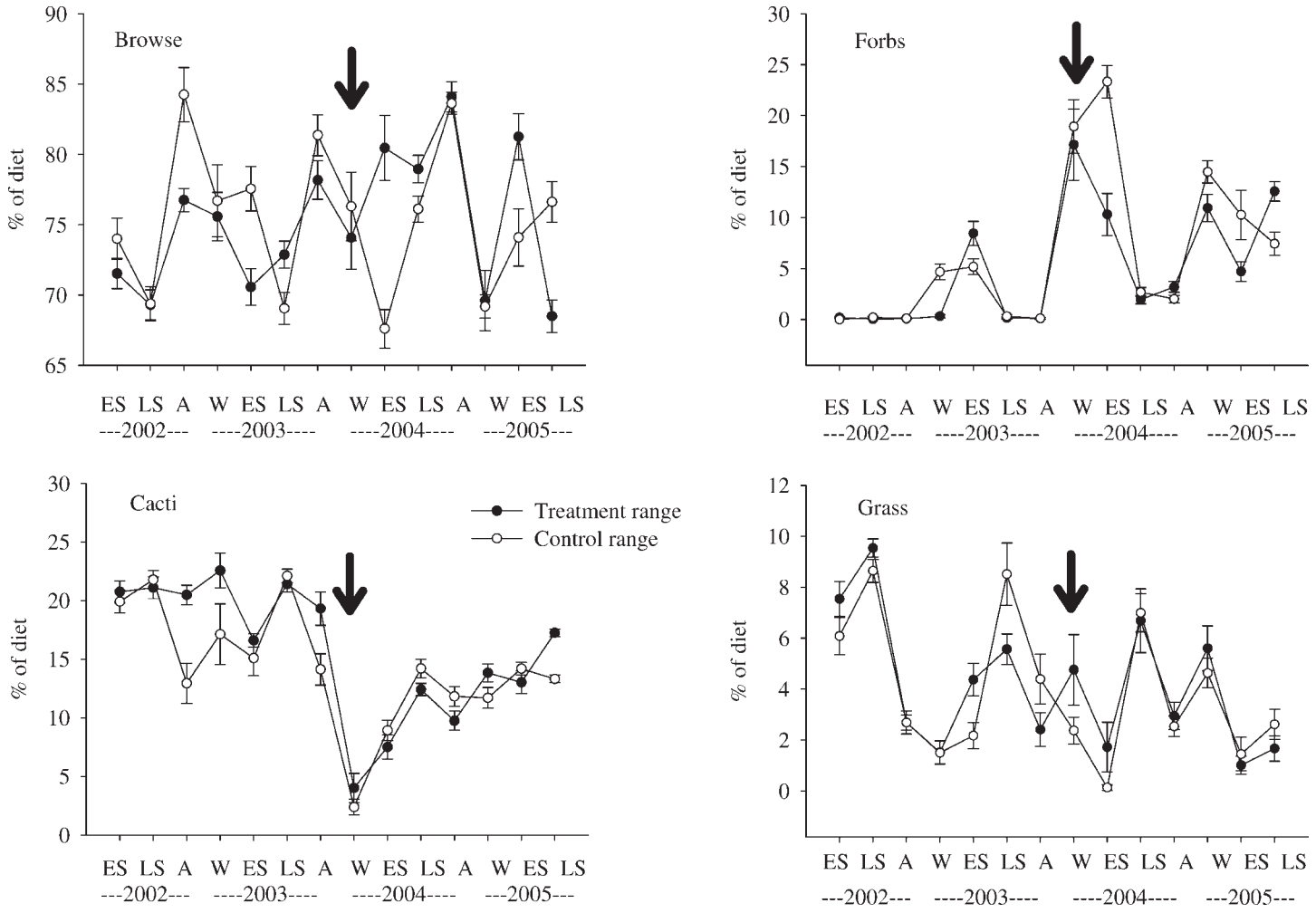

Figure 6. Seasonal composition of desert bighorn sheep diets by forage class (browse, grass, cacti, and forbs) in the Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona, USA, early summer (ES) 2002 to late summer (LS) 2005; W = winter, A = autumn. Error bars represent standard error; arrow indicates initiation of water removal.

Table 2. Mean percent relative density of plant species in the winter (Jan–Mar) diet of female desert bighorn sheep in the treatment (Sierra Pinta) and control (Cabeza Prieta) mountain ranges during pre- (2002–2003) and posttreatment (2004–2005), Cabeza Prieta National Wildlife Refuge, Arizona, USA.

	Treatment mountain range				Control mountain range			
	Pretreatment		Posttreatment		Pretreatment		Posttreatment	
Species	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Grasses								
Big galleta	1.1	0.46	3.2	0.64	0.9	0.36	1.9	0.35
Bush muhly (*Muhlenbergia porteri*)	0.5	0.33	1.3	0.31	0.6	0.23	0.3	0.13
Red brome (*Bromus rubens*)	0.0	0.00	0.8	0.28	0.0	0.00	1.4	0.43
Three-awn	0.0	0.00	0.0	0.00	0.0	0.00	0.2	0.09
Browse								
Brittlebush	0.0	0.00	0.7	0.70	0.0	0.00	0.0	0.00
Burro bush (*Hymenoclea salsola*)	0.0	0.00	0.2	0.08	0.0	0.00	0.1	0.05
Canyon ragweed (*Ambrosia ambrosioides*)	0.0	0.00	0.4	0.15	0.0	0.00	0.5	0.23
Catclaw acacia	0.0	0.00	0.0	0.00	0.0	0.00	0.3	0.26
Desert hackberry (*Celtis pallida*)	0.0	0.00	0.5	0.19	0.1	0.09	0.1	0.06
Desert lavender	3.7	1.26	9.5	0.91	4.2	0.96	8.6	0.77
Ephedra	2.8	0.69	3.7	0.56	3.8	0.80	3.6	0.46
Fairy duster (*Calliandra eriophylla*)	1.0	0.63	0.9	0.28	0.0	0.00	0.0	0.00
Globe mallow	0.0	0.00	6.5	0.88	0.0	0.00	7.7	0.78
Golden-eye (*Viguiera parishii*)	0.0	0.00	0.8	0.31	0.0	0.00	0.7	0.33
Ironwood	23.3	2.48	10.1	1.10	20.7	1.14	10.2	0.85
Janusia	0.3	0.17	1.5	0.40	0.5	0.18	2.2	0.45
Jojoba (*Simmondsia chinensis*)	0.0	0.00	0.1	0.08	0.2	0.13	0.2	0.08
Mesquite	0.8	0.37	0.1	0.07	0.0	0.00	0.2	0.14
Palo verde	20.4	3.31	6.9	0.96	22.7	0.99	6.9	0.79
Ratany	0.9	0.39	1.1	0.34	0.1	0.09	0.5	0.16
Silverbush	3.1	1.05	7.5	0.82	5.6	0.99	7.9	0.81
White bursage	0.9	0.31	0.7	0.23	1.5	0.37	1.0	0.24
Chuparosa (*Justicia californica*)	0.1	0.11	0.1	0.04	0.0	0.05	0.3	0.12
Wolfberry (*Lycium* spp.)	0.7	0.34	0.6	0.14	0.7	0.25	0.6	0.17
Wright's buckwheat	17.7	1.78	17.2	1.09	16.7	0.97	17.5	0.75
Succulents								
Barrel cactus	0.2	0.13	0.2	0.08	0.3	0.10	0.3	0.10
Fishhook mammillaria and cholla	22.4	1.52	9.8	1.13	16.9	2.58	7.8	1.04
Forbs								
Bedstraw (*Galium stellatum*)	0.0	0.00	2.3	0.54	0.0	0.00	3.1	0.67
Bladder stem (*Eriogonium inflatum*)	0.0	0.00	0.2	0.09	0.0	0.00	0.4	0.13
Borage	0.3	0.16	5.2	0.61	4.4	0.73	6.2	0.55
Filaree	0.0	0.00	2.5	0.42	0.3	0.13	4.8	0.44
Indian wheat	0.0	0.00	5.0	0.79	0.0	0.00	4.0	0.84
Lupine	0.0	0.00	0.3	0.13	0.0	0.00	0.6	0.17
Vetch (*Astragalus nuttallianus*)	0.0	0.00	0.1	0.06	0.0	0.00	0.2	0.08

early summer ($F_{1,6} = 0.042$, $P = 0.844$) or late summer ($F_{1,6} = 3.34$, $P = 0.117$; Fig. 10).

Similar to 95% home-range areas, we found a evidence for a range × treatment interaction comparing changes in 50% home-range area ($F_{1,28} = 2.96$, $P = 0.096$). We found a treatment effect for winter and autumn 50% home-range areas. Home-range area during winter increased in the treatment range from 1.7 ± 0.438 km^2 to 2.7 ± 0.044 km^2 and decreased from 1.3 ± 0.445 km^2 to 0.7 ± 0.105 km^2 in the control range from pretreatment to posttreatment ($F_{1,6} = 6.26$, $P = 0.046$). During autumn, 50% home range increased from 1.7 ± 0.083 km^2 to 3.2 km^2 in the treatment range and remained constant at 1.6 ± 0.259 km^2 in the control range from pretreatment to posttreatment ($F_{1,6} = 11.25$, $P = 0.015$). We did not find a treatment effect for early summer ($F_{1,6} = 0.066$, $P = 0.805$) or late summer ($F_{1,6} = 1.26$, $P = 0.305$; Fig. 10).

In the treatment range, seasonal 95% and 50% home-range areas during pretreatment declined with increasing seasonal precipitation (95% kernel $r^2 = 0.401$, $\beta = -1.005 \pm 0.501$, $P = 0.092$; 50% kernel $r^2 = 0.550$, $\beta = -1.384 \pm 0.511$, $P = 0.035$). In the control range, 95% home-range area also declined with increasing seasonal precipitation ($r^2 = 0.404$, $\beta = -1.029 \pm 0.510$, $P = 0.090$); however, there was little evidence of a relationship between 50% home-range area and precipitation ($r^2 = 0.351$, $\beta = -1.024 \pm 0.569$, $P = 0.122$; Fig. 11). During posttreatment, 95% and 50% home-range area was not associated with seasonal precipitation in the treatment range (95% home-range area $r^2 = 0.358$, $\beta = 0.398 \pm 0.238$, $P = 0.156$; 50% home-range area $r^2 = 0.283$, $\beta = 0.431 \pm 0{,}307$, $P = 0.219$) or in the control range (95% home-range area $r^2 = 0.140$, $\beta = -0.482 \pm 0.532$, $P = 0.408$; 50% home-range area $r^2 = 0.105$, $\beta = -0.531 \pm 0.694$, $P = 0.479$). However, there were 2 influential data points corresponding to autumn 2004, the season with the highest precipitation (Fig. 11). After exclusion of these points (Fig. 11), the regression

Table 3. Mean percent relative density of plant species in the early summer (Apr–Jun) diet of female desert bighorn sheep in the treatment (Sierra Pinta) and control (Cabeza Prieta) mountain ranges during pre- (2002–2003) and posttreatment (2004–2005), Cabeza Prieta National Wildlife Refuge, Arizona, USA.

	Treatment mountain range				Control mountain range			
	Pretreatment		Posttreatment		Pretreatment		Posttreatment	
Species	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Grasses								
Big galleta	4.4	0.66	0.1	0.09	3.5	0.47	0.1	0.09
Bush muhly	0.1	0.06	0.0	0.00	0.3	0.10	0.0	0.00
Grama grass	0.0	0.00	0.3	0.11	0.2	0.08	0.3	0.11
Red brome	1.3	0.42	0.0	0.00	0.0	0.00	0.0	0.00
Three-awn	0.1	0.04	0.1	0.06	0.1	0.04	0.1	0.06
Browse								
Brittlebush	6.7	0.57	2.7	0.50	6.4	0.87	2.7	0.50
Burro bush	0.0	0.02	0.0	0.00	0.2	0.07	0.0	0.00
Canyon ragweed	0.2	0.09	0.2	0.11	0.6	0.18	0.2	0.11
Catclaw acacia	1.5	0.58	6.9	0.79	1.5	0.59	6.9	0.79
Desert lavender	4.2	0.42	6.1	0.74	3.8	0.39	6.1	0.74
Ephedra	7.5	0.92	3.5	0.53	7.5	0.80	3.5	0.53
Fairy duster	0.2	0.09	0.0	0.00	0.1	0.05	0.0	0.00
Globe mallow	2.8	0.58	5.5	0.97	1.8	0.48	5.5	0.97
Ironwood	19.7	1.52	13.1	0.93	21.7	1.30	13.1	0.93
Janusia	1.7	0.33	2.2	0.48	2.4	0.37	2.2	0.48
Jojoba	0.1	0.06	0.0	0.00	0.2	0.06	0.0	0.00
Ocotillo	0.0	0.00	1.7	0.32	0.0	0.00	1.7	0.32
Palo verde	16.5	0.65	15.3	0.79	18.9	0.69	15.3	0.79
Ratany	2.3	0.35	2.1	0.41	3.3	0.42	2.1	0.41
Silverbush	1.7	0.27	4.8	0.54	1.9	0.31	4.8	0.54
White bursage	1.8	0.35	0.2	0.10	1.1	0.18	0.2	0.10
Wolfberry	0.3	0.07	0.1	0.04	0.2	0.07	0.1	0.04
Wright's buckwheat	3.8	0.83	17.1	0.59	4.2	0.77	17.1	0.59
Succulents								
Barrel cactus	0.4	0.16	0.5	0.15	0.3	0.10	0.5	0.15
Desert agave	0.1	0.07	0.7	0.19	0.3	0.10	0.7	0.19
Fishhook mammillaria and cholla	18.2	0.64	8.6	0.90	16.8	0.96	8.6	0.90
Forbs								
Bedstraw	0.5	0.15	0.1	0.09	0.2	0.08	0.1	0.09
Bladder stem	0.1	0.06	0.0	0.00	0.0	0.00	0.0	0.00
Borage	0.3	0.08	4.8	0.64	0.0	0.00	4.8	0.64
Desert marigold (*Baileya multiradiata*)	0.3	0.10	0.2	0.12	0.3	0.11	0.2	0.12
Filaree	2.7	0.68	0.4	0.19	2.1	0.51	0.4	0.19
Golondrina	0.2	0.09	1.1	0.30	0.2	0.12	1.1	0.30
Indian wheat	0.0	0.00	1.1	0.47	0.0	0.00	1.1	0.47
Lupine	0.2	0.09	0.4	0.23	0.0	0.00	0.4	0.23

coefficients for the control range were $r^2 = 0.589$, $\beta = -1.313 \pm 0.548$, $P = 0.075$ for 95% home-range area and $r^2 = 0.447$, $\beta = -1.468 \pm 0.816$, $P = 0.146$ for the 50% home-range area. Exclusion of these 2 data points did not change the results for the treatment range (95% home-range area $r^2 = 0.261$, $\beta = 0.512 \pm 0.430$, $P = 0.300$; 50% home-range area $r^2 = 0.227$, $\beta = 0.598 \pm 0.552$, $P = 0.340$).

Movement rate.—In the treatment range, pretreatment movement rates were higher during early summer ($\bar{x} \pm$ SE; 37.5 ± 3.5 m/hr) and late summer (46.7 ± 4.7 m/hr), whereas posttreatment movement rates were highest during winter (50.8 ± 1.6 m/hr) and autumn (42.2 m/hr; Fig. 12). In the control range, pretreatment movement rates were highest during winter (41.3 ± 8.1 m/hr) and early summer (51.4 ± 7.0 m/hr); during posttreatment, movement rates were highest in late summer (37.3 ± 1.1 m/hr) and autumn (38.4 m/hr). We found a treatment effect comparing winter movement rates ($F_{1,6} = 5.85$, $P = 0.052$). Winter movement rates in the treatment range increased by 35% from 37.5 ± 5.2 m/hr to 50.5 ± 4.2 m/hr, whereas winter movement rate in the control range decreased 24% from 42.9 ± 5.1 m/hr to 32.8 ± 2.1 m/hr from pretreatment to posttreatment. We did not find treatment effects for early summer ($F_{1,6} = 0.105$, $P = 0.757$), late summer ($F_{1,6} = 0.047$, $P = 0.836$), or autumn ($F_{1,6} = 3.26$, $P = 0.121$).

The relationship between movement rates and seasonal precipitation were similar to that observed for home-range area and precipitation. During pretreatment, movement rates declined with increasing precipitation in the treatment range ($r^2 = 0.461$, $\beta = -0.684 \pm 0.302$, $P = 0.064$) but not in the control range ($r^2 = -0.089$, $\beta = -0.265 \pm 0.346$, $P = 0.472$), and during posttreatment, movement rates were not associated with precipitation in either the treatment range ($r^2 = 0.061$, $\beta = -0.087 \pm 0.152$, $P = 0.593$) or control range ($r^2 = 0.001$, $\beta = -0.018 \pm 0.216$, $P = 0.937$). Exclusion of 2 outliers for autumn 2004 did not

Table 4. Mean percent relative density of plant species in the late-summer (Jul–Sep) diet of female desert bighorn sheep in the treatment (Sierra Pinta) and control (Cabeza Prieta) mountain ranges during pre- (2002–2003) and posttreatment (2004–2005), Cabeza Prieta National Wildlife Refuge, Arizona, USA.

	Treatment mountain range				Control mountain range			
	Pretreatment		Posttreatment		Pretreatment		Posttreatment	
Species	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Grasses								
Big galleta	6.6	0.53	3.2	0.57	7.0	0.55	3.5	0.47
Bush muhly	0.1	0.07	0.2	0.09	0.1	0.05	0.3	0.15
Grama grass	0.6	0.19	1.3	0.39	1.4	0.36	1.2	0.30
Browse								
Brittlebush	1.5	0.28	0.5	0.22	1.0	0.21	0.3	0.14
Burro bush	0.0	0.00	0.1	0.07	0.1	0.04	0.1	0.05
Canyon ragweed	0.2	0.06	0.3	0.09	0.5	0.15	0.4	0.15
Catclaw acacia	0.0	0.00	0.0	0.00	0.0	0.00	0.1	0.04
Desert hackberry	0.0	0.00	0.3	0.10	0.0	0.00	0.6	0.16
Desert lavender	3.9	0.38	4.9	0.50	3.3	0.38	4.9	0.52
Ephedra	3.3	0.50	2.2	0.38	3.6	0.37	3.6	0.45
Fairy duster	0.1	0.08	0.5	0.16	0.1	0.09	0.1	0.04
Globe mallow	0.3	0.14	5.2	0.55	0.2	0.16	5.3	0.46
Golden-eye	0.0	0.00	0.0	0.00	0.1	0.05	0.0	0.00
Holly-leaf bursage (*Ambrosia ilicifolia*)	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.02
Ironwood	31.5	1.19	22.4	1.39	30.2	1.20	23.9	1.28
Janusia	5.5	0.42	6.3	0.78	5.3	0.53	5.6	0.57
Jojoba	0.1	0.07	0.2	0.13	0.2	0.09	0.2	0.09
Mesquite	8.0	1.58	7.3	1.20	6.6	1.30	7.0	0.75
Palo verde	11.4	0.98	12.6	0.52	12.7	1.17	11.9	0.59
Ratany	2.0	0.30	0.9	0.24	1.2	0.32	0.9	0.18
Silverbush	2.3	0.40	4.7	0.49	2.7	0.37	6.4	0.44
Trixis (*Trixis californica*)	0.0	0.00	0.0	0.03	0.0	0.00	0.1	0.07
White bursage	1.0	0.17	0.4	0.14	0.9	0.18	0.6	0.15
Chuparosa	0.0	0.00	0.1	0.05	0.1	0.06	0.0	0.00
Wolfberry	0.3	0.10	0.2	0.09	0.2	0.09	0.1	0.06
Wright's buckwheat	0.0	0.00	4.1	0.54	0.1	0.05	4.4	0.50
Succulents								
Barrel cactus	0.4	0.11	0.6	0.17	0.6	0.18	0.8	0.16
Desert agave	0.2	0.11	0.1	0.05	0.1	0.06	0.3	0.12
Fishhook mammillaria and cholla	20.7	0.54	14.1	0.56	21.2	0.45	12.6	0.34
Forbs								
Bladder stem	0.0	0.00	0.0	0.00	0.1	0.05	0.0	0.00
Borage	0.0	0.02	2.8	0.39	0.0	0.03	2.6	0.52
Desert marigold	0.0	0.00	0.1	0.05	0.0	0.00	0.4	0.14
Filaree	0.1	0.06	0.2	0.09	0.2	0.08	0.4	0.12
Golondrina	0.0	0.00	3.8	0.75	0.0	0.00	1.2	0.35
Lupine	0.0	0.00	0.2	0.07	0.0	0.00	0.2	0.09

influence the association between movement rate and precipitation.

Distance to water catchments.—Bighorn sheep in the treatment range were an average (± SE) of 2,910 ± 218 m and 2,644 ± 117 m from the nearest water catchment during pre- and posttreatment, respectively, whereas animals in the control range were an average of 2,522 ± 204 m and 2,456 ± 217 m from the nearest catchment during pre- and posttreatment, respectively (Fig. 13). Distance to catchment during winter in the treatment range decreased by 25% from 3,245 ± 424 m to 2,426 ± 184 m, whereas in the control range, distance to catchment decreased 9% from 2,672 ± 393 m to 2,437 ± 407 m from pretreatment to posttreatment ($F_{1,6} = 6.21$, $P = 0.047$). We did not find evidence of a treatment effect for early summer ($F_{1,6} = 0.028$, $P = 0.873$), late summer ($F_{1,6} = 0.649$, $P = 0.451$), or autumn ($F_{1,6} = 0.011$, $P = 0.751$; Fig. 13).

Mean distance of female desert bighorn sheep to the nearest catchment was not associated with precipitation in the treatment range during pretreatment ($r^2 = 0.034$, $\beta = -0.177 \pm 386$, $P = 0.663$) or posttreatment ($r^2 = 0.214$, $\beta = 0.120 \pm 154$, $P = 0.296$). Distance of animals in the control range from catchments was not associated with precipitation during pretreatment ($r^2 = 0.041$, $\beta = 0.073 \pm 0.144$, $P = 0.629$). In contrast, during posttreatment, distance to the nearest catchment increased with increasing precipitation ($r^2 = 0.433$, $\beta = 0.138 \pm 0.071$, $P = 0.100$).

Survival

Sheep were radiocollared for an average (± SD) of 462 ± 303 days in the treatment range and 515 ± 446 days in the control range. Sheep-years of radiomonitoring were 24.1 and 25.4 for the treatment and control ranges, respectively. Seven radiocollared animals died in each mountain range during pretreatment: 4 in

Table 5. Mean percent relative density of plant species in the autumn (Oct–Dec) diet of female desert bighorn sheep in the treatment (Sierra Pinta) and control (Cabeza Prieta) mountain ranges during pre- (2002–2003) and posttreatment (2004–2005), Cabeza Prieta National Wildlife Refuge, Arizona, USA.

	Treatment mountain range				Control mountain range			
	Pretreatment		Posttreatment		Pretreatment		Posttreatment	
Species	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Grasses								
Big galleta	1.6	0.19	2.1	0.40	1.6	0.19	1.2	0.31
Bush muhly	0.3	0.12	0.6	0.28	0.3	0.12	0.7	0.24
Grama grass	0.5	0.14	0.2	0.13	0.5	0.14	0.7	0.24
Three-awn	0.1	0.04	0.0	0.00	0.1	0.04	0.0	0.00
Browse								
Burro bush	0.0	0.03	0.0	0.04	0.0	0.03	0.2	0.09
Desert hackberry	0.0	0.00	0.2	0.09	0.0	0.00	0.2	0.10
Desert lavender	5.8	0.58	10.8	0.88	5.8	0.58	11.6	1.45
Ephedra	1.7	0.32	2.8	0.63	1.7	0.32	3.0	0.61
Fairy duster	0.0	0.00	0.4	0.23	0.0	0.00	0.0	0.03
Globe mallow	0.0	0.00	10.0	1.32	0.0	0.00	3.9	0.52
Ironwood	22.8	0.95	21.7	1.37	22.8	0.95	25.4	0.84
Janusia	3.5	0.51	4.8	0.81	3.5	0.51	3.8	0.55
Jojoba	0.2	0.07	0.1	0.07	0.2	0.07	0.2	0.09
Lotus (*Lotus rigidis*)	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
Mesquite	1.7	0.45	0.0	0.00	1.7	0.45	0.0	0.00
Palo verde	19.0	0.83	14.8	0.72	19.0	0.83	16.3	0.64
Ratany	0.9	0.28	1.0	0.36	0.9	0.28	1.1	0.44
Silverbush	3.4	0.42	5.3	0.72	3.4	0.42	8.4	0.85
White bursage	2.6	0.39	0.9	0.27	2.6	0.39	0.8	0.23
Chuparosa	0.1	0.03	0.0	0.03	0.1	0.03	0.2	0.08
Wolfberry	0.4	0.09	0.6	0.22	0.4	0.09	0.3	0.13
Wright's buckwheat	15.0	0.76	9.6	0.47	15.0	0.76	7.9	0.42
Succulents								
Fishhook mammillaria and cholla	20.1	0.72	9.7	0.82	20.1	0.72	11.8	0.84
Forbs								
Bedstraw	0.0	0.00	0.9	0.26	0.0	0.00	0.5	0.18
Borage	0.1	0.04	3.2	0.51	0.1	0.04	2.0	0.37

each mountain range in 2002 and 3 in each mountain range in 2003. During pretreatment, 5 of 7 mortalities in the treatment range were during hot seasons (early summer and late summer), whereas in the control range 3 of 7 mortalities were during hot seasons (Table 8).

During posttreatment, there were 3 mortalities in the treatment range and one in the control range. All 4 mortalities during posttreatment were during hot seasons. Eight of the 10 mortalities in the treatment range were during early summer and late summer, and 2 were during winter. In the control range, 4 of the 8 mortalities were during early summer and late summer, 3 during autumn, and one during winter.

Survival rates were highest in both mountain ranges during cool seasons in both pretreatment (treatment range $\bar{x}$ [± SE] = 0.902 ± 0.098; control range $\bar{x} = 0.792 \pm 0.210$) and posttreatment (treatment range $\bar{x} = 0.923 \pm 0.078$; control range $\bar{x} = 0.931 \pm 0.069$). Mean survival rate during the hot seasons was lower during pretreatment (treatment range $\bar{x} = 0.569 \pm 0.236$; control range $\bar{x} = 0.745 \pm 0.095$) than during posttreatment (treatment range $\bar{x} = 0.759 \pm 0.134$; control range $\bar{x} = 0.940 \pm 0.061$) in both mountain ranges (Table 9). Hot- and cool-season survival rates did not change in response to removal of water sources ($F_{1,14} = 0.191$, $P = 0.669$).

During pretreatment in the treatment range, proximate causes of mortality were due to mountain lion predation ($n = 2$), falls ($n = 3$), and unknown causes ($n = 5$; Table 8). During pretreatment in the control range, mortalities were attributed to mountain lion predation ($n = 1$), disease ($n = 1$), falls ($n = 1$), and unknown causes ($n = 5$). During posttreatment, we were unable to determine the cause of the 3 mortalities in the treatment range; however, based on the condition of the carcass, all 3 animals had not been depredated or scavenged and we found 2 of 3 in a bedded position <80 m from a drained water catchment. In addition, in July 2005 we found an uncollared female in a similar bedded position <20 m from a drained water catchment in the treatment range. Conversely, of mortalities in the treatment range during pretreatment, the nearest to a water source was 1.5 km ($\bar{x} = 3.3$ km, range = 1.5–6.2 km). In the control range during

Table 6. Morisita–Horn similarity indices for seasonal desert bighorn sheep diets in the Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona, USA, 2002–2005.

Yr	Winter	Early summer	Late summer	Autumn
2002		0.994	0.999	0.942
2003	0.979	0.963	0.992	0.986
2004	0.981	0.938	0.986	0.972
2005	0.971	0.974	0.945	

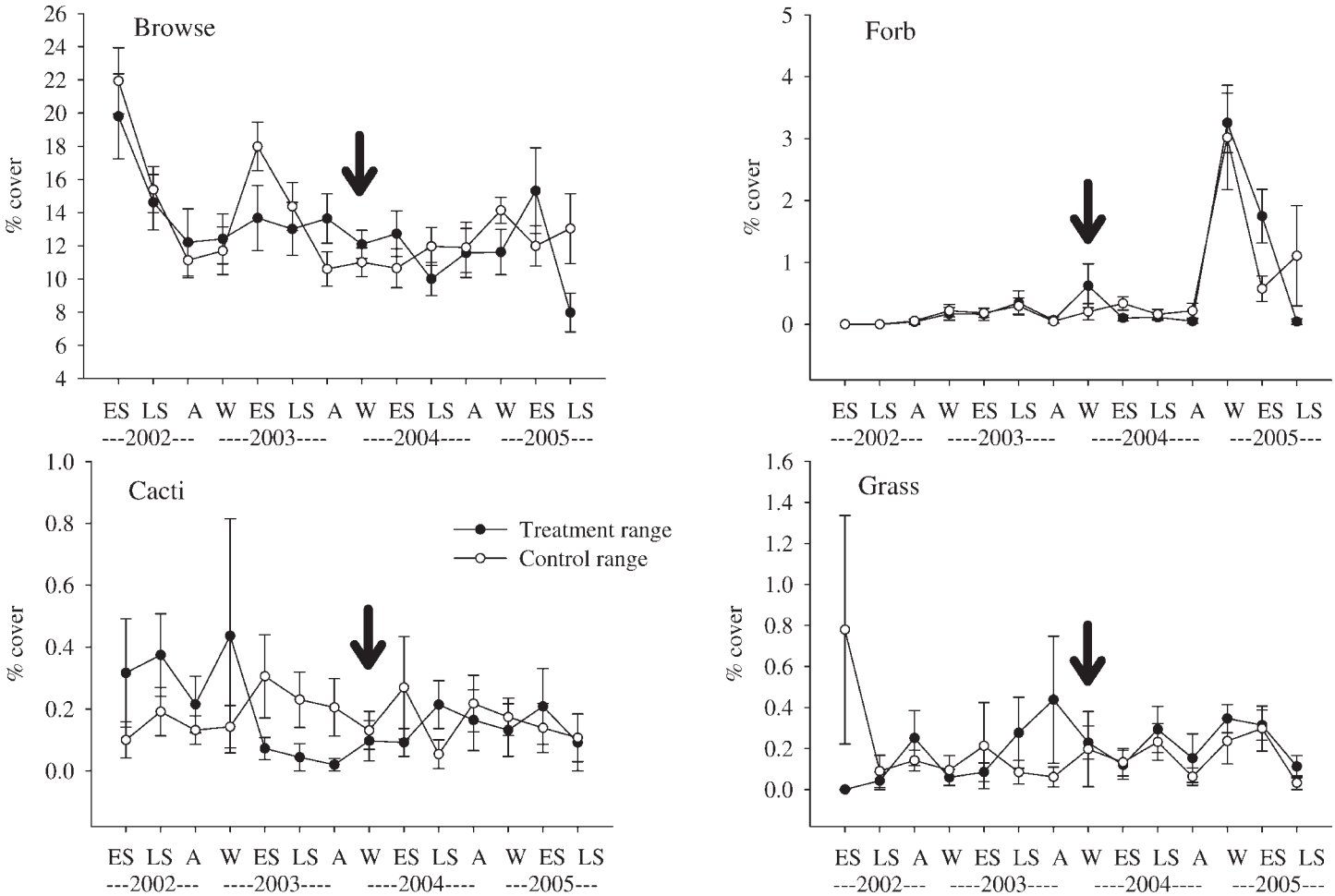

Figure 7. Seasonal vegetative cover by forage class (browse, grass, cacti, and forbs) of desert bighorn sheep foraging locations in the Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona, USA, early summer (ES) 2002 to late summer (LS) 2005; W = winter, A = autumn. Error bars represent standard error; arrow indicates initiation of water removal.

posttreatment, the radiocollar on the single animal that died failed in July 2005. We located the carcass of this animal in late September 2005 and it exhibited similar characteristics (i.e., carcass intact and unscavenged) as those found in the treatment range. In addition, we found that 39% of skulls of mortalities ($n = 7$) during this study showed signs consistent with chronic sinusitis. We found 15 additional adult bighorn sheep skulls (9 M and 6 F) during this study; 6 of these skulls had abnormalities consistent with chronic sinusitis.

Survival rates were lowest in both mountain ranges during pretreatment and increased during posttreatment. Survival (± SE) during pretreatment and posttreatment in the treatment range was 0.227 ± 0.127 and 0.772 ± 0.142, respectively. In the control range, survival during pretreatment was 0.272 ± 0.134 and survival after treatment was 0.883 ± 0.110. Annual survival rate did not change in response to removal of water sources ($F_{1,6} = 1.308$, $P = 0.296$; Fig. 14).

Annual survival rates were associated with the current and previous year's precipitation ($r^2 = 0.948$). Survival rates increased as the current year's total precipitation increased ($\beta = 0.0534 \pm 0.002$, $P < 0.001$; Fig. 15) and the total precipitation during the previous year increased ($\beta = 0.0267 \pm 0.002$, $P < 0.001$). Annual survival rates decreased as the average daily temperature increased during winter ($r^2 = 0.469$, $\beta = -0.047 \pm 0.021$, $P = 0.061$).

Productivity and Recruitment

Lamb:female ratios in the treatment range were stable in 2002 (0.292 ± 0.041 [SE]), 2003 (0.284 ± 0.581), and 2004 (0.320 ± 0.103), then declined in 2005 (0.118 ± 0.048), whereas lamb:female ratios in the control range were similar in 2002 (0.136 ± 0.016) and 2005 (0.146 ± 0.048) and also similar in 2003 (0.356 ± 0.059) and 2004 (0.352 ± 0.029). We found little evidence of a treatment effect for lamb:female ratios ($F_{1,6} = 0.166$, $P = 0.698$; Fig. 16). There was little evidence for a relationship between lamb:female ratios and increases in annual precipitation ($r^2 = 0.324$, $P = 0.141$; Fig. 17).

There was evidence of a treatment effect for yearling:female ratios ($F_{1,6} = 9.97$, $P = 0.019$). However, there was an overall increase in the total yearling:female ratio in the treatment range from pretreatment to posttreatment, whereas there was an overall decrease in the yearling:female ratio in the control range during this same time (Fig. 18). The yearling:female ratio in the treatment range decreased between 2002 (0.010 ± 0.026) and 2003 (0.040 ± 0.011), increased between 2003 and 2004 (0.267 ± 0.087), then declined between 2004 and 2005 (0.223 ± 0.076). In the control

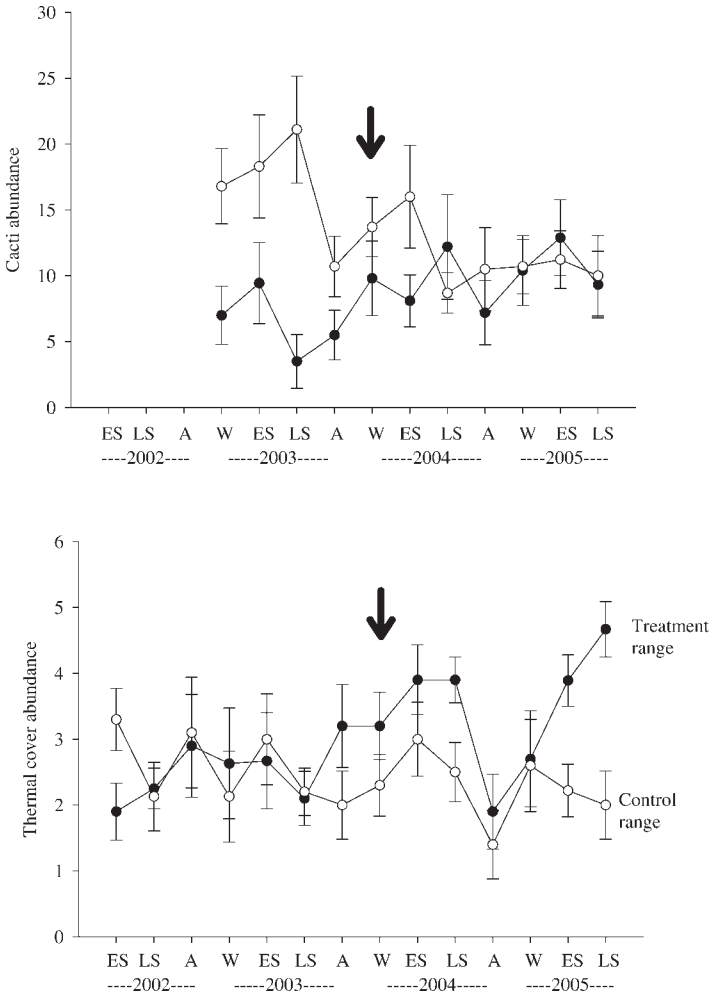

Figure 8. Seasonal abundance of cacti and thermal cover of desert bighorn sheep foraging locations in the Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona, USA, early summer (ES) 2002 to late summer (LS) 2005; W = winter, A = autumn. Error bars represent standard error; arrow indicates initiation of water removal.

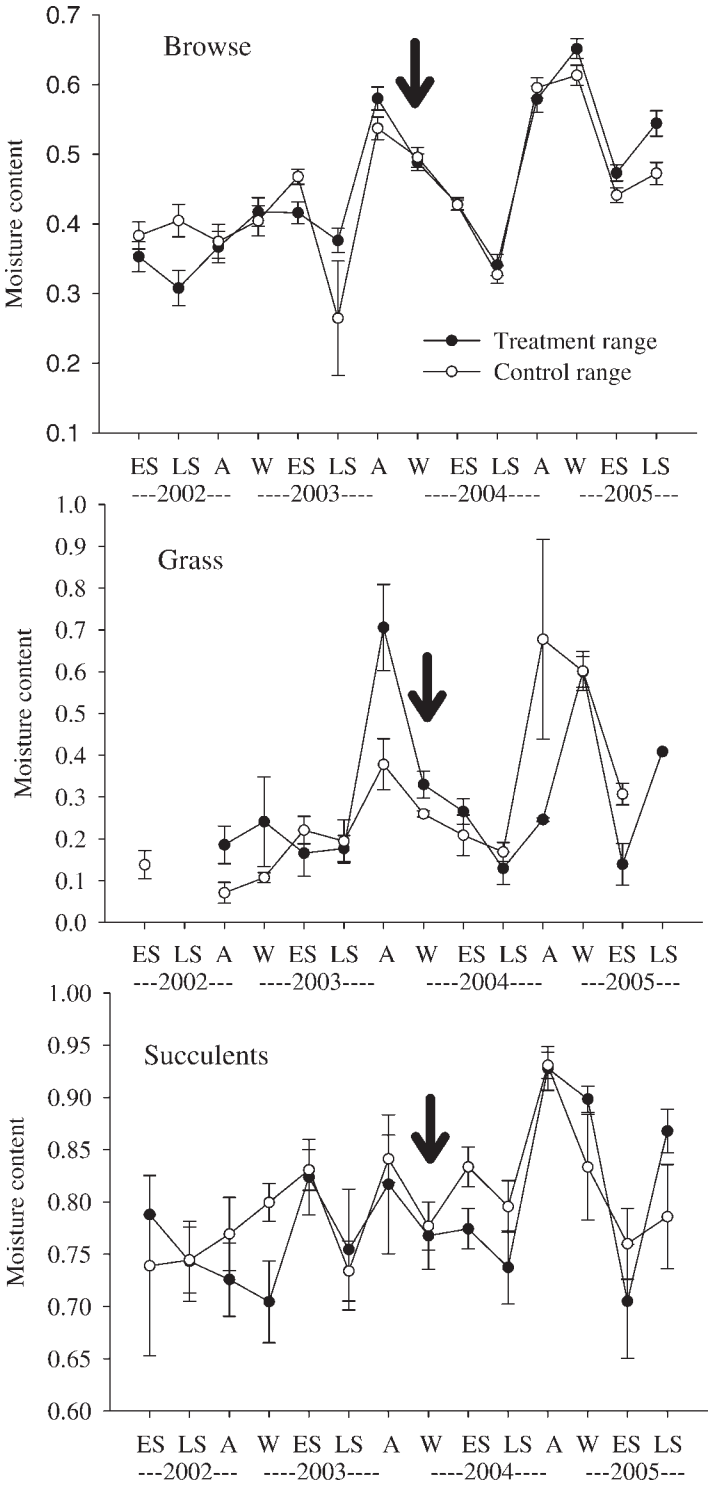

Figure 9. Seasonal moisture content by forage class (browse, grass, and cacti) of plants in the diets of desert bighorn sheep in the Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona, USA, early summer (ES) 2002 to late summer (LS) 2005; W = winter, A = autumn. Error bars represent standard error; arrow indicates initiation of water removal.

range, yearling:female ratios decreased between 2002 (0.273 ± 0.076) and 2003 (0.172 ± 0.069) and between 2003 and 2004 (0.086 ± 0.012), then increased between 2004 and 2005 (0.192 ± 0.055). The yearling:female ratio increased with increasing early summer precipitation ($r^2 = 0.393$, $P = 0.096$; Fig. 19).

DISCUSSION

Removal of water catchments in the treatment range did not result in predicted changes in diet, foraging area selection, home-range size, movement rates, mortality, productivity, and recruitment. Female desert bighorn sheep used areas with more thermal cover when catchments were removed, but diet and other foraging area characteristics did not change appreciably with removal of water. We did not document changes in home-range area, movement rates, or distance of sheep from water during hotter months. In addition, we did not document increased mortality or a change in lamb:female or yearling:female ratios after removal of water catchments.

Our prediction that animals in the treatment range would increase their consumption of succulents during posttreatment was not supported by our results. However, browse consumption in the treatment range increased by 10% during early summer of posttreatment, corresponding with the increase in moisture content of browse due to above-normal precipitation. The increased consumption of browse at a time when early summer

Table 7. Mean seasonal moisture content of the 7 most important forage species and cacti (i.e., barrel cactus and agave) found in the diets of desert bighorn sheep in the Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona, USA, 2002–2005.

	Winter		Early summer		Late summer		Autumn	
Species	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Agave	0.78	0.07	0.76	0.06	0.73	0.07	0.81	0.10
Barrel cactus	0.90	0.03	0.91	0.05	0.90	0.04	0.93	0.10
Big galleta grass	0.23	0.10	0.25	0.09	0.20	0.08	0.34	0.22
Desert lavender	0.60	0.07	0.50	0.07	0.47	0.11	0.62	0.11
Ironwood	0.48	0.05	0.52	0.04	0.54	0.06	0.59	0.07
Fishhook mammillaria	0.74	0.15	0.66	0.15	0.65	0.14	0.78	0.19
Palo verde	0.42	0.04	0.47	0.07	0.44	0.06	0.49	0.06
Wright's buckwheat	0.43	0.19	0.38	0.08	0.21	0.06	0.38	0.16
Silverbush	0.47	0.19	0.41	0.07	0.37	0.24	0.49	0.19

moisture content was high may have helped compensate for lack of water in catchments in the treatment range. We detected no other significant changes in the diet of desert bighorn sheep in the treatment range in response to removal of the anthropogenic water sources. These limited changes suggest that when water catchments were removed during an abnormally wet period, forage played a more important role in influencing life-history characteristics we studied than did water catchments.

The relative proportions of browse, grass, forbs, and cacti in the diet of female desert bighorn sheep on the CPNWR were similar to those observed in other studies of desert bighorn sheep. Browse represented the majority of diet during all seasons of our study and has been documented to be the primary forage class observed in diets in studies of desert bighorn sheep in Arizona (Seegmiller and Ohmart 1981, Krausman et al. 1989, Miller and Gaud 1989, Etchberger and Krausman 1998), California (Oehler et al. 2003), New Mexico (Sandoval 1979), Texas (Brewer 2001), and Sonora, Mexico (Tarango 2000). However, grasses were found in higher proportions seasonally in other studies in Arizona (Hansen and Martin 1973, Dodd and Brady 1988, Morgart 1990, Holt et al. 1992) and dominated seasonal diets of bighorn sheep in Nevada (Barrett 1964, Brown et al. 1977) and California (Bleich et al. 1997). In the Virgin Mountains, Arizona, and Baja California Sur, Mexico, forbs dominated the diets of bighorn sheep (Sanchez 1976, Smith and Krausman 1987) and in Texas forbs and browse were equally important in bighorn sheep diets (Fulbright et al. 2001).

Cacti represented the second highest proportion of the seasonal diets in our study from early summer 2002, autumn 2003, late summer and autumn 2004, and early summer and late summer 2005, roughly corresponding to all seasons during the drought period and the hot seasons during posttreatment. Consumption of fishhook mammillaria, barrel cactus, saguaro, and buckhorn cholla by desert bighorn sheep has been previously documented (Seegmiller and Ohmart 1982, Miller and Gaud 1989, Warrick and Krausman 1989, Tarango 2000, Brewer 2001). Some studies have documented increased foraging on cacti during winter (Krausman et al. 1989, Warrick and Krausman 1989). However, many studies documented increased consumption of cacti during early summer and late summer (Seegmiller and Ohmart 1982, Miller and Gaud 1989, Etchberger and Krausman 1998, Tarango 2000, Brewer 2001). In addition to fishhook mammillaria, barrel cactus, and buckhorn cholla, we found desert agave in bighorn sheep diets during early summer and late summer. Consumption of the central portion of desert agave was observed by Tarango (2000), who speculated that the central portion was high in moisture content. Mean moisture content of desert agave collected during our study was >70% during all seasons, confirming speculation by Tarango (2000). Barrel cactus, buckhorn cholla, and fishhook mammillaria have low (typically <5%) protein content, particularly when compared to other available forage species (Morgart et al. 1986, Seegmiller et al. 1990). Therefore, desert bighorn sheep are likely consuming these species for their

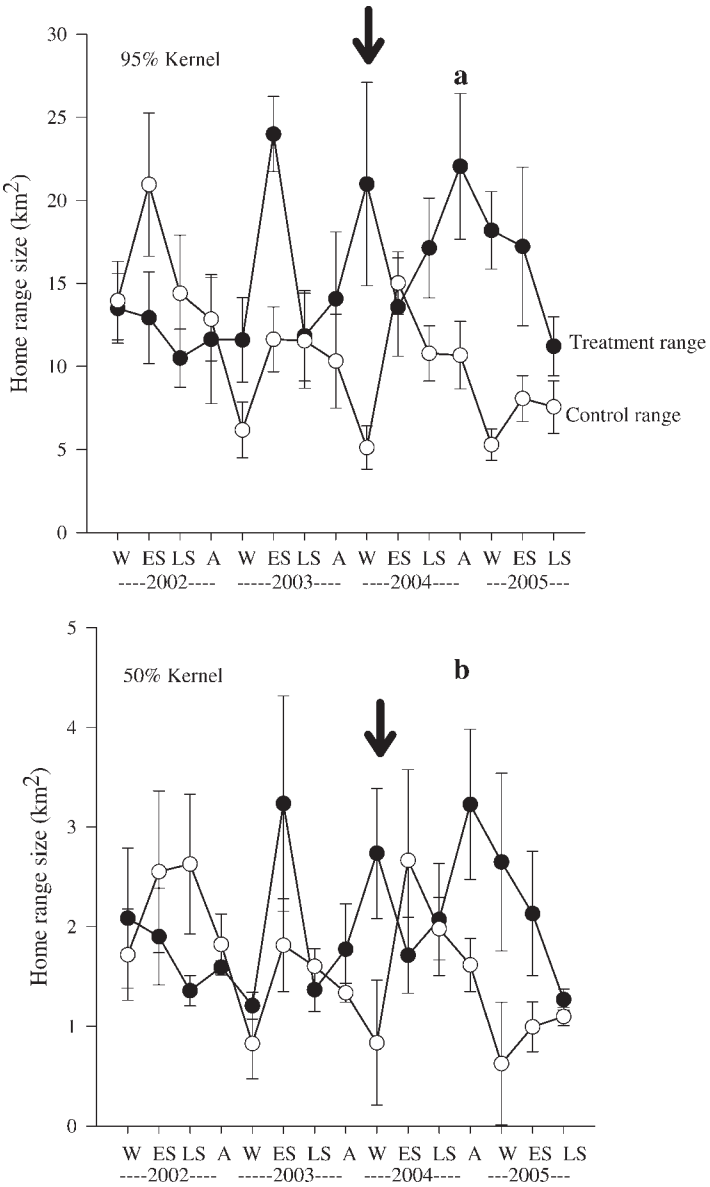

Figure 10. Mean seasonal (a) 95% and (b) 50% kernel home-range size (km^2) of female desert bighorn sheep in the Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona, USA, early summer (ES) 2002 to late summer (LS) 2005; W = winter, A = autumn. Error bars represent standard error; arrow indicates initiation of water removal.

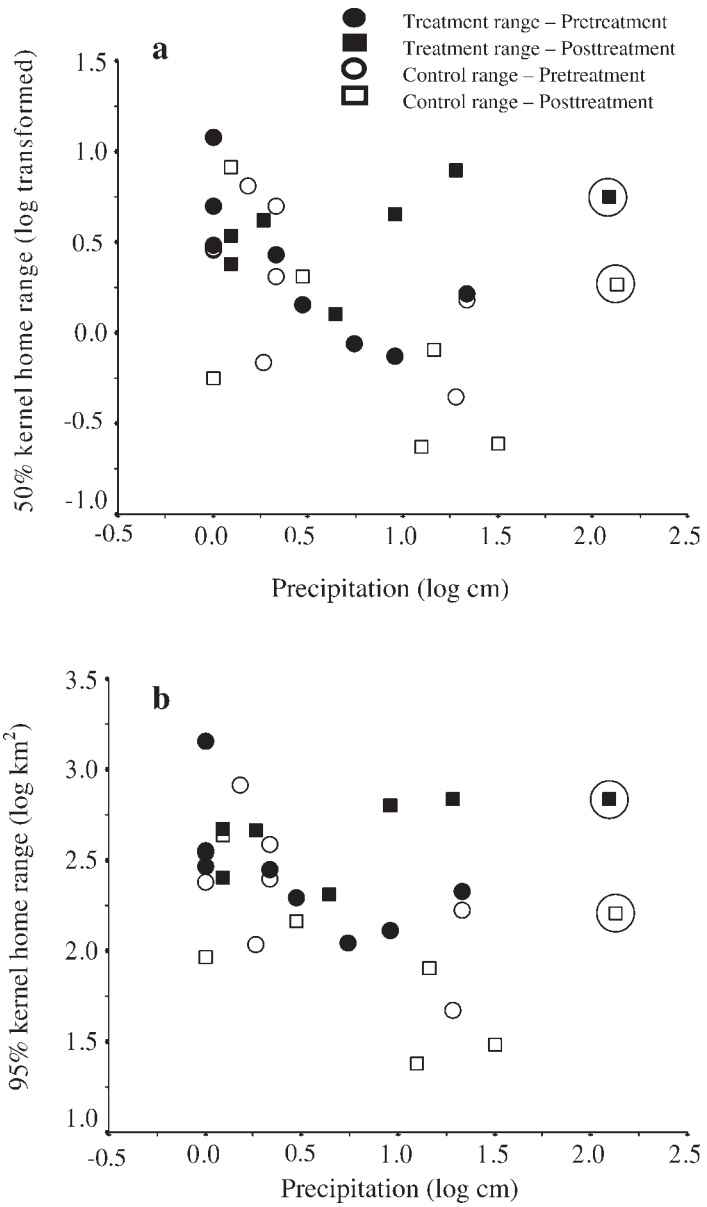

Figure 11. Relationship between mean seasonal (a) 50% and (b) 95% kernel home-range areas (log transformed) of female desert bighorn sheep and seasonal precipitation, Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona, USA, early summer 2002 to late summer 2005. Two autumn 2004 outliers are identified with extra circle.

high (70–90%) moisture content rather than for nutritional content (Oehler et al. 2003).

We found support for our prediction that thermal cover would be higher in the posttreatment foraging areas of bighorn sheep in the treatment range. Use of foraging areas with a higher abundance of thermal cover by bighorn sheep in the treatment range during the summer seasons of posttreatment may be indicative of a behavioral response to removal of water sources. Use of vegetation for shade is a widely recognized mechanism of ungulates in arid environments that reduces heat loads, helps maintain a temperature gradient between the body and the environment, which results in convective heat loss, and reduces the need for evaporative cooling, thus minimizing water loss

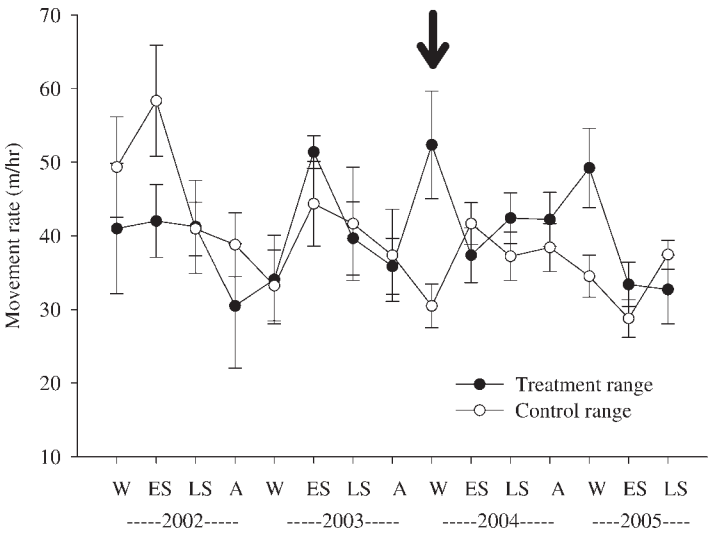

Figure 12. Mean seasonal movement rates (m/hr) for female desert bighorn sheep in the Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona, USA, early summer (ES) 2002 to late summer (LS) 2005; W = winter, A = autumn. Error bars represent standard error; arrow indicates initiation of water removal.

(Anthony 1972, Sargeant et al. 1994, Tull et al. 2001). Ambient temperatures on the CPNWR have been documented up to 3.8° C lower in areas shaded by vegetation than in unshaded areas (Simmons 1969, Cain et al. 2008).

Our prediction that foraging areas of bighorn sheep in the treatment range would have higher vegetative cover and succulent abundance was not supported by our results. Overall vegetation cover of the foraging areas used by desert bighorn sheep between the treatment and control ranges remained constant between pre- and posttreatment. Cacti abundance in the foraging areas used by bighorn sheep in the control range were lower during posttreatment (non-drought) than in areas used during pretreatment

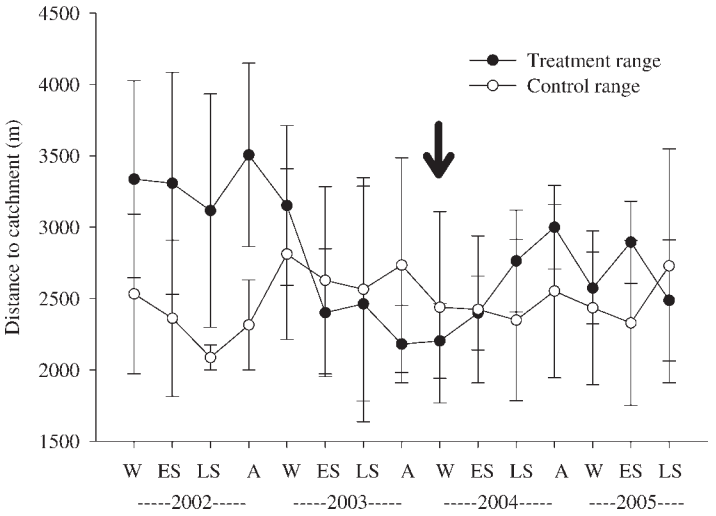

Figure 13. Mean seasonal distance (m) to nearest water catchment for female desert bighorn sheep in the Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona, USA, early summer (ES) 2002 to late summer (LS) 2005; W = winter, A = autumn. Error bars represent standard error; arrow indicates initiation of water removal.

Table 8. Year, season, and probable causes of mortalities observed for radiocollared adult female desert bighorn sheep in the Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona, USA, 2002–2005.

		Winter		Early summer		Late summer		Autumn	
Mountain range	Yr	Probable cause	*n*	Probable cause	*n*	Probable cause	*n*	Probable cause	*n*
Sierra Pinta	2002					Unknown[a]	1		
						Lion predation	1		
						Fall	2		
	2003	Lion predation	1	Unknown[a]	1				
		Fall	1						
	2004					Unknown[b]	1		
	2005			Unknown[b]	1	Unknown[b]	1		
Cabeza Prieta Mountains	2002			Lion predation	1			Unknown[a]	2
				Fall	1				
	2003	Disease[c]	1	Unknown[b]	1			Unknown[a]	1
	2004								
	2005			Unknown[b,d]	1				

[a] Unable to determine cause of mortality due to scavenging of carcass.
[b] Unable to determine cause of mortality; condition or position of carcass indicated non–predation-related mortality.
[c] Positive serum test for bovine parainfluenza 3.
[d] Radiocollar stopped functioning during early summer 2005; mortality found late summer 2005; exact season of mortality unknown.

(drought), whereas cacti abundance was relatively constant in forage plots of bighorn sheep in the treatment range during this same time. It is interesting that we did not observe a similar decrease in cacti abundance in forage plots used by animals in the treatment range during posttreatment, when overall forage conditions improved due to increased precipitation. However, if the lack of a response to improving forage conditions was related to removal of water catchments, we also would have expected to find a corresponding increase in the proportion of cacti in the diet of animals in the treatment range. Given less than ideal weather conditions during our study (extremely dry pretreatment vs. abnormally wet posttreatment), a smaller decrease in proportion of cacti in the diet of animals in the treatment range from pre- to posttreatment could have also been indicative of a treatment response. We did not observe either an increase or smaller decrease in the proportion of cacti in the diet of animals in the treatment range.

The high proportion of cacti in the diet during winter and autumn of 2002–2003 may have been a consequence of the reduced availability of forbs and grasses due to the drought, rather than dietary preference during these cooler seasons. Increases in precipitation during posttreatment resulted in higher availability of forbs and grasses, likely resulting in an increased consumption of forbs and grasses and a decreased consumption of cacti during this period. Similar seasonal shifts with increased forb and grass consumption during winter and late summer have been documented in other populations of desert bighorn sheep in Arizona (Seegmiller and Ohmart 1981, Miller and Gaud 1989, Holt et al. 1992), California (Bleich et al. 1997), New Mexico (Sandoval 1979), and Sonora, Mexico (Tarango 2000). The increase in forage moisture content likely minimized the need for animals in the treatment range to dramatically change their diets or foraging areas in response to catchment removal. Moisture content of browse species was typically >30%, grasses >15%, and cacti >70%.

Desert bighorn sheep require a minimum 3–4% of their body mass in water per day during summer (Turner 1973). It has been proposed that desert bighorn sheep in areas devoid of perennial water sources obtain sufficient moisture from their forage, but there have not been any studies to determine the minimum forage moisture content necessary for desert bighorn sheep to maintain water balance during times when water sources (ephemeral or perennial) are lacking (Mendoza 1976, Watts 1979, Alderman et al. 1989, Warrick and Krausman 1989, Cain et al. 2006). Although there has been relatively little research on the physiology of thermoregulation and water balance in desert ungulates of North America, there are data from African and Middle Eastern ungulates that inhabit arid areas. For example, the Arabian oryx (*Oryx leucoryx*) in Oman is independent of free-water sources at temperatures ≤31° C when forage moisture content is ≥35% and at temperatures ≤40° C when forage moisture content is ≥50% (Stanley Price 1989). Gemsbok (*Oryx gazella*) are independent of free-water sources when forage moisture content is ≥33% (Knight 1991), and impala (*Aepyceros melampus*) are independent of free-water sources when forage moisture content is ≥67% (Jarman 1973). The lowest mean seasonal forage moisture content we observed was 33%, 12%, 63%, and 73% for browse, grass, forbs, and succulents, respectively.

Table 9. Hot-season (early summer [ES] and late summer [LS]) and cool-season (autumn [A] and winter [W]) survival rates of female desert bighorn sheep in the Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona, USA, 2002–2005.

	Sierra Pinta		Cabeza Prieta Mountains	
Season	Survival rate	95% CI	Survival rate	95% CI
W02	1.00	1.00–1.00	1.00	1.00–1.00
ES02–LS02	0.333	0.083–0.713	0.651	0.254–0.911
A02–W03	0.804	0.316–0.973	0.584	0.245–0.859
ES03–LS03	0.804	0.316–0.973	0.840	0.384–0.978
A03–W04	0.845	0.392–979	0.862	0.432–0.981
ES04–LS04	0.893	0.515–0.985	1.00	1.00–1.00
A04–W05	1.00	1.00–1.00	1.00	1.00–1.00
ES05–LS05	0.626	0.289–0.873	0.879	0.473–0.983

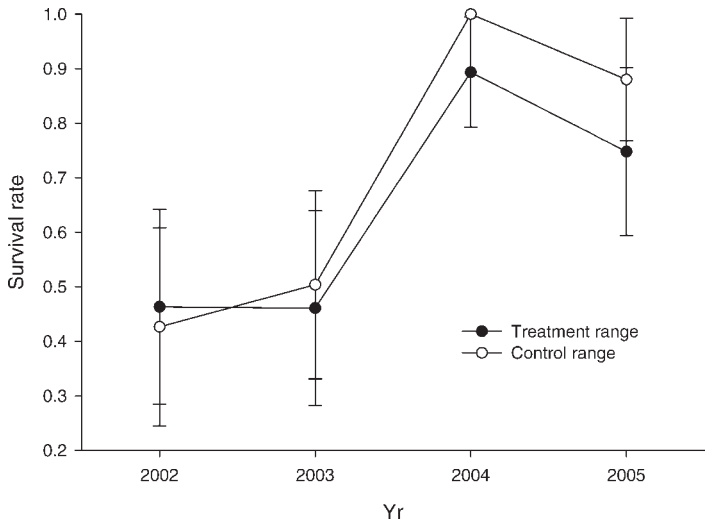

Figure 14. Annual adult desert bighorn sheep survival in the Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona, USA, 2002–2005. Error bars represent standard error.

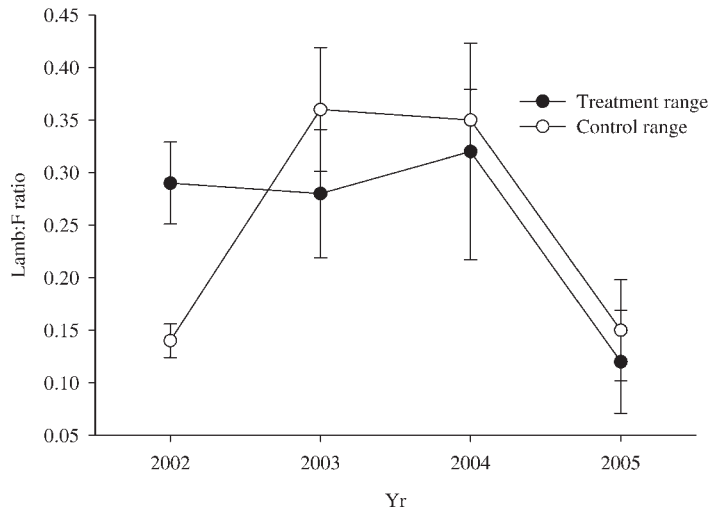

Figure 16. Annual lamb:female ratio of desert bighorn sheep in the Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona, USA, 2002–2005. Error bars represent standard error.

We caution any interpretation that desert bighorn sheep also would be able to maintain water balance with similar forage moisture contents as for the African species described above. These species have a wide range of water requirements and employ a variety of physiological, morphological, and behavioral mechanisms for thermoregulation and water balance, making any extrapolation to desert bighorn sheep tenuous at best (Cain et al. 2006). In the absence of physiological studies on desert bighorn sheep under the environmental conditions they commonly encounter in native ranges, the minimum forage moisture content required by desert bighorn sheep to maintain water balance will remain unknown. In addition, minimum forage moisture requirements will likely vary by sex, age class, and reproductive status. Also, minimum forage moisture necessary for survival of an adult animal is likely lower than that required for successful reproduction and juvenile survival.

Our predictions that removal of water catchments in the treatment range would influence home-range size, movement rates, and distance to catchments were not supported. Both 95% and 50% kernel home-ranges increased in the treatment range and decreased in the control range during winter and autumn from pretreatment to posttreatment, whereas we did not find changes in the 95% and 50% kernel home ranges during the early summer or late summer for either mountain range. If the presence of water catchments influenced the home-range size of female desert

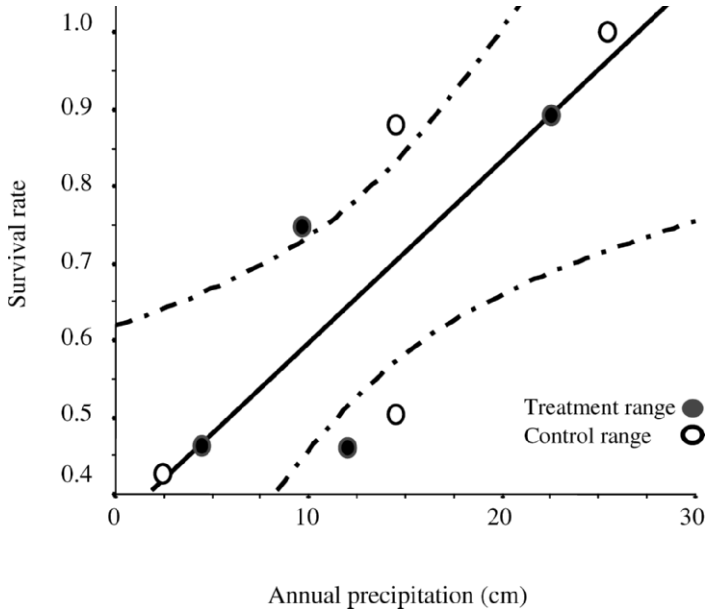

Figure 15. Least-squares linear regression line and 95% confidence intervals for annual precipitation and annual survival rate of female desert bighorn sheep in the Sierra Pinta (●) and Cabeza Prieta Mountains (○), Cabeza Prieta National Wildlife Refuge, Arizona, USA, 2002–2005.

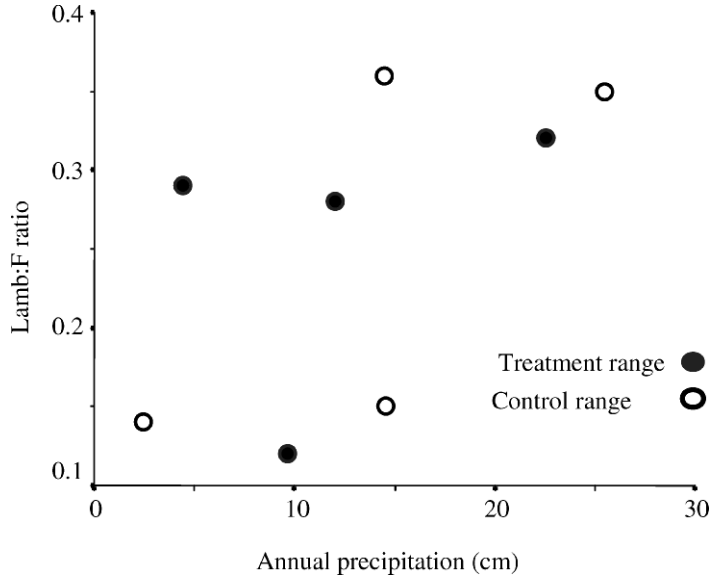

Figure 17. Relationship between annual precipitation and lamb:female ratio of desert bighorn sheep in the Sierra Pinta (●) and Cabeza Prieta Mountains (○), Cabeza Prieta National Wildlife Refuge, Arizona, USA, 2002–2005.

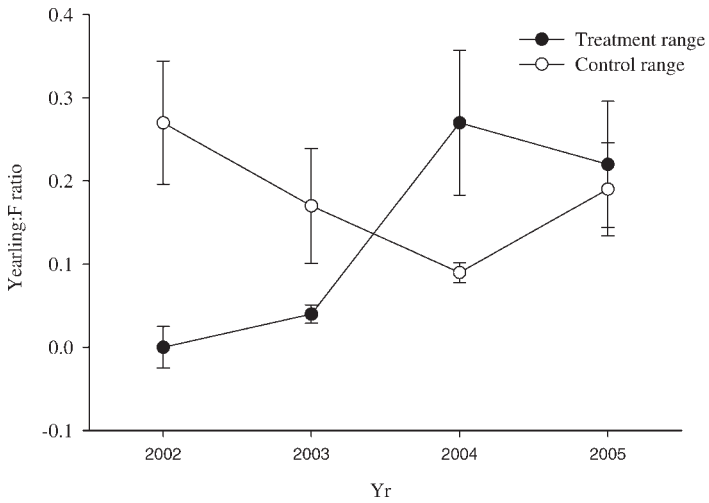

Figure 18. Annual yearling:female ratio of desert bighorn sheep in the Sierra Pinta and Cabeza Prieta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona, USA, 2002–2005. Error bars represent standard error.

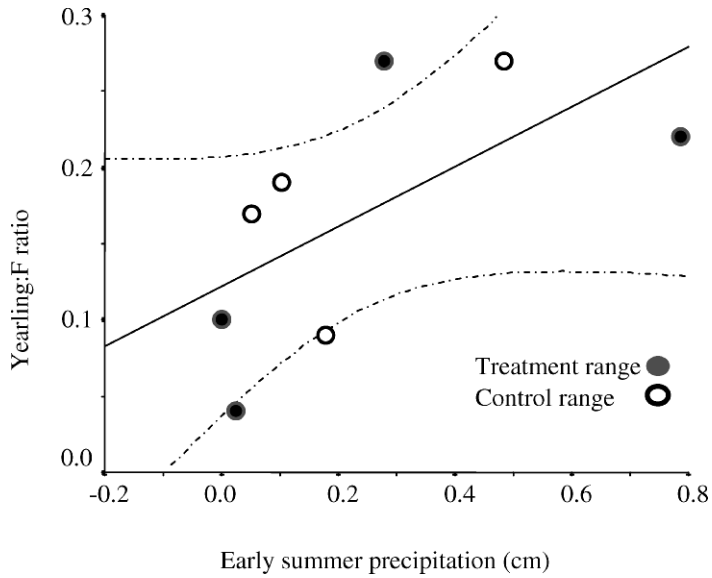

Figure 19. Least-squares linear regression line and 95% confidence intervals for early summer (Apr–Jun) precipitation and yearling:female ratios of desert bighorn sheep in the Sierra Pinta (●) and Cabeza Prieta Mountains (○), Cabeza Prieta National Wildlife Refuge, Arizona, USA, 2002–2005.

bighorn sheep in the treatment range, we expected an increase in home ranges in summer.

Our data did not support our prediction that we would find increased movement rates after removal of water catchments. In the treatment range, pretreatment movement rates were highest during early summer and late summer and posttreatment movement rates were highest during winter and autumn. Movement rates in the control range were highest in winter and late summer during pretreatment and in late summer and autumn during posttreatment. If movement rates of female desert bighorn sheep are influenced by presence of catchments, we would have expected an increase in movement rates during summer when the influence of water catchments should be most evident.

The general trend we observed of decreasing home-range size and movement rates with increasing precipitation likely reflects the response of female desert bighorn sheep to changes in forage quantity and quality resulting from precipitation. During seasons with high precipitation, animals are more likely to be able to meet their forage needs in a smaller area than during seasons with little precipitation. The close relationship between plant abundance and precipitation is particularly evident in arid environments (Beatley 1969, Noy-Meir 1973, Goldberg and Turner 1986). In the Sonoran Desert, forage growth and biomass are related to precipitation (Goldberg and Turner 1986, Marshal et al. 2005*a*). Nutritional analysis of forage species commonly observed in the diet of female desert bighorn sheep indicate that forage quality was highest during seasons with the highest precipitation (Morgart et al. 1986, Krausman et al. 1989, Seegmiller et al. 1990). Crude protein and in vitro dry matter digestibility tend to be highest during periods with increasing precipitation and forage growth (i.e., wet seasons) and lowest during periods of low precipitation (Krausman et al. 1990, Bleich et al. 1992, Marshal et al. 2005*b*).

Animals in highly productive environments are typically able to meet their resource needs in a smaller area relative to those inhabiting less productive areas (Jewell 1966, Harestad and Bunnell 1979). This relationship between habitat productivity and home-range size has been observed in ungulates inhabiting a wide variety of environments including temperate, semiarid, and arid environments (Leslie and Douglas 1979, Rubenstein 1989, Beier and McCullough 1990, Tufto et al. 1996, Brashares and Arcese 2002). In the desert southwestern United States, desert mule deer (Rautenstrauch and Krausman 1989, Relyea et al. 2000), Sonoran pronghorn (Hervert et al. 2005), and desert bighorn sheep (Krausman et al. 1989, Oehler et al. 2003) inhabiting areas with lower quality or quantity of forage resources tend to have larger home ranges than those in more productive areas. Movement rates of ungulates are also associated with forage conditions (Owen-Smith and Novellie 1982). For example, female desert bighorn sheep in the Little Harquahala Mountains, Arizona, where forage resource quantity and quality were lower, had higher seasonal movement rates than did animals in the adjacent Harquahala Mountains, which had higher-quality forage resources (Warrick and Krausman 1987, Krausman et al. 1989). Home ranges and movement rates of ungulates can also vary seasonally in response to seasonal changes in forage resources, with animals having higher movement rates and larger home-range areas during seasons when forage resources are limited (Owen-Smith and Novellie 1982, Knight 1991, Tufto et al. 1996, Corp et al. 1998, Anderson et al. 2005). Desert bighorn sheep home ranges and movement rates tend to be highest during seasons with low precipitation (Warrick and Krausman 1987, Alderman et al. 1989, Krausman et al. 1989, Locke 2003).

Contrary to our predictions, the distance from GPS locations of female desert bighorn sheep to catchments did not generally increase in the treatment range after removal of water from the catchments. In fact, the only significant change in the distance of bighorn sheep from water catchments was an 820-m decrease in the treatment range from pretreatment to posttreatment. Many studies of habitat use of desert bighorn sheep document a relationship between their distribution and the location of

perennial water sources, with the distribution of females being more closely tied to the location of perennial water sources than that of males due to the smaller body size of females and higher water demands related to gestation and lactation (Blong and Pollard 1968, More and Sahni 1978, Hassan et al. 1988, Bleich et al. 1997). In addition, studies of desert bighorn sheep habitat use document a decrease in distance to the nearest perennial water source during summer, with increasing distances during autumn and winter (Irvine 1969, Leslie and Douglas 1979, Bates and Workman 1983, Wakeling and Miller 1990*a*, Locke 2003). However, other studies failed to find similar relationships between distribution of sheep and location of perennial water sources (Krausman and Leopold 1986, Krausman and Etchberger 1995). We did not document seasonal changes in bighorn sheep distribution relative to water sources during any year of our study in either the treatment or control ranges.

The overall lack of response in home-range size, movement rates, and distance to the nearest water catchment after removal of water sources and the trend of decreasing home-range sizes and movements with increases in precipitation suggests that forage conditions played a larger role in determining home-range area and movement rates during our study than did presence of water catchments. Similarly, Oehler et al. (2003) suggest that differences in home-range size between the Old Dad and Panamint mountains in the Mojave Desert, California, were the result of differential precipitation patterns and their influence on forage abundance and quality.

We did not find a decrease in survival rate of female desert bighorn sheep due to removal of water from catchments. Mortality was highest during pretreatment and was likely related to the severe drought at the beginning of the study. Most mortalities in the treatment range were during early summer and late summer of both pretreatment and posttreatment, whereas mortalities in the control range were more evenly distributed throughout the year.

Survival rates we observed were positively associated with precipitation. Adult survival increased with increasing annual precipitation and with precipitation during the previous year. Our observation that the lowest survival rates were during the pretreatment drought when water was maintained in catchments indicates that during the severe drought of 2002, the presence of water catchments was not sufficient to prevent mortalities of desert bighorn sheep and a lack of forage quality and quantity was likely the primary limiting factor of the population during this time (Smith and LeCount 1979, Krausman and Leopold 1986, Alderman et al. 1989, Krausman et al. 1989). However, mortalities observed during posttreatment occurred with above-normal precipitation and may have been related to removal of water from catchments.

Although we did not find a significant change in survival in response to removal of water from catchments, the proximity of animals that died during posttreatment to the drained catchments does raise questions about the impact of water removal. The locations (<80 m from drained catchment) of the 2 collared animals and one uncollared animal we found in the treatment range during posttreatment were much closer to water catchments than were the locations of any of the animals that died in either mountain range during the drought in pretreatment.

Causes of mortality were similar for each mountain range during both pretreatment and posttreatment. However, we were only able to establish proximate causes of mortality and only for a proportion of the total mortalities were we able to determine the cause. Relationships between water availability and the ultimate causes of mortality are unknown. In addition, the prevalence of skull abnormalities consistent with chronic sinusitis was similar in skulls recovered from each mountain range. Although chronic sinusitis has been associated with mortality in desert bighorn sheep (Paul and Bunch 1978), it is unknown if this condition influenced mortalities we observed during this study.

We assumed that survival rates of radiocollared animals in this study were representative of the population survival rate. However, telemetry collars can cause injuries to study animals, which can influence body condition and affect behavior, reproductive success, and survival (Bleich et al. 1990, Côté et al. 1998, Murray and Fuller 2000, Krausman et al. 2004, Bleich et al. 2007). Even in the absence of injuries, there may be an increase in energetic cost associated with carrying a telemetry collar that may affect study animals (Bleich et al. 2007); therefore, we cannot exclude the possibility that removal of water may have resulted in higher mortality rates in radiocollared animals than in the population at large.

The energetic investment required to successfully raise a lamb in a desert environment may limit a female's ability to successfully rear a lamb the following year. Krausman et al. (1989) found that females in the Harquahala Mountains, Arizona, that were successful in rearing a lamb to >6 months seldom were successful in rearing a lamb the following year. In contrast, in the Virgin Mountains, Arizona, Morgart (1990) found that females were successful in rearing lambs in successive years. The yearling:female and lamb:female ratios in our study support observations by Krausman et al. (1989). Yearling:female ratios in 2002, which represent the portion of lambs surviving from 2001, were high in the control range and lamb:female ratios were low; when yearling:female ratios decreased in 2003 and 2004, lamb:female ratios were the highest we observed during our study. In 2005, when yearling:female ratios increased again we observed a decline in lamb:female ratios. We observed a similar pattern in the treatment range; years with high yearling:female ratios typically had low lamb:female ratios, with the exception of 2004, which had both high lamb:female and yearling:female ratios.

Our data also failed to support our prediction that lamb:female and yearling:female ratios would decrease in response to removal of water from catchments. Lamb survival in desert bighorn sheep is greatly influenced by precipitation during autumn of the previous year, likely through its influence on forage quality and quantity (Douglas and Leslie 1986, Wehausen et al. 1987, Krausman et al. 1999). Douglas (2001) found that maximum May temperatures and winter precipitation 2 years before lambs were born was associated with lamb survival, which he speculated was related to the condition of the female. Both timing and amount of precipitation can have significant influence on forage production, which affects body condition of females and can influence the likelihood of successfully rearing a lamb through the first summer (Robinson and Forbes 1968, Douglas 2001). In addition, nutritional quality of forage and water balance of females affect

milk production and may affect growth rates and survival of young (Hossaini-Hilali et al. 1994; Landete-Castillejos et al. 2001, 2003). This relationship between precipitation, forage production, and offspring survival has also been found for desert mule deer and pronghorn (Smith and LeCount 1979, Leopold and Krausman 1991, Bright and Hervert 2005, Bristow et al. 2006).

Lamb:female ratios were relatively high in both mountain ranges in 2004, then decreased in both ranges in 2005. If the removal of water sources negatively impacted lamb survival, we would have expected a decrease in the treatment range only, not in both mountain ranges. Given the relationships found between precipitation and lamb survival and juvenile recruitment in other desert bighorn sheep populations, it is unusual that the autumn and winter seasons of 2004, with above-normal precipitation were followed by the low lamb:female ratios we observed in 2005 in both mountain ranges. However, cloudy and cold winter weather has been associated with higher incidence of pneumonia and internal parasites, resulting in lower lamb survival (Hansen 1960). Douglas (2001) found a negative relationship between precipitation during April and lamb survival in Canyonlands National Park, Utah. Holl and Bleich (1983) found a similar inverse relationship between lamb:female ratio and precipitation during lambing, which they attributed to weather-related mortality of lambs. Similarly, we observed precipitation in January and February 2005 that was >2 times the normal amount and may have contributed to the low lamb:female ratios observed.

Precipitation has been related to population dynamics of herbivores that inhabit semiarid and arid environments (Caughley et al. 1985, Fryxell 1987, Owen-Smith 1990, Marshal et al. 2002). Drought and winter precipitation have also been related to population declines in other desert bighorn sheep populations in Arizona (Monson 1960; McKinney et al. 2001, 2006). McKinney et al. (2001) found that drought-related decreases in winter precipitation were associated with declines in desert bighorn sheep recruitment rates. McKinney et al. (2001) found lower yearling numbers on surveys 1.5 years following years with low winter precipitation. However, we did not find any change in yearling:female ratios due to removal of water. Higher-quality forage conditions associated with above-average precipitation during posttreatment, increases in forage moisture content, and availability of naturally occurring sources of free water in the treatment range likely minimized any impact of removing water from catchments on survival rates and lamb:female and yearling:female ratios.

Differences in the weather conditions observed during pre- and posttreatment likely influenced our results. The study began during the worst drought in southwestern Arizona in 107 years. The period from September 2001 to August 2002 was the driest on record for this region. Furthermore, our study ended during an abnormally wet period. The period from October 2004 to September 2005 was the 21st wettest on record for this region during this period of time (National Oceanic and Atmospheric Administration 2002, 2005). The increase in precipitation that coincided with removal of water sources during posttreatment may have obviated the need for female desert bighorn sheep to respond to removal of water catchments by changing their diet, foraging areas, movement rates, or home-range areas. During posttreatment, increases in forage moisture content and availability of naturally occurring sources of free water in the treatment range likely minimized any impact of removing water catchments.

The frequency of drought in Arizona and the Southwest makes effective planning by wildlife management agencies difficult. The influence of water catchments likely varies, depending on weather and forage conditions. During abnormally wet years, forage moisture content and naturally occurring sources of free water are likely sufficient to meet water requirements of desert bighorn sheep. During drought years, quantity and quality of available forage may be more of a limiting factor than availability of free water (Douglas and Leslie 1986, Krausman and Leopold 1986, Alderman et al. 1989, Krausman et al. 1989). Based on our data, we suggest that precipitation and vegetation have a stronger influence on life-history characteristics of desert bighorn sheep than do water catchments during abnormal climatic conditions. Although we conducted our study during periods of severe drought and above-average rainfall, these conditions are commonly observed in the Sonoran Desert; normal periods are less common. For example, long-term (1969–2006) mean annual precipitation recorded at Tacna, Arizona (approx. 64 km N of our study area), was 10.5 cm. Annual precipitation during 10 of 38 years was ≥125% of average and 13 of 38 was ≤75% of average. Given the unpredictable and extremely variable precipitation in the desert Southwest, it will be difficult to determine the relative importance of perennial sources of free water and preformed water in forage for any particular year.

MANAGEMENT IMPLICATIONS

The lack of significant changes in diet, foraging-area characteristics, movement rates, home-range size, mortality, productivity, and juvenile recruitment in response to removal of water catchments suggests that during years with above-normal precipitation, perennial sources of freestanding water are not limiting to desert bighorn sheep in the treatment range and have little influence during times when forage moisture content is high. Conversely, during periods of drought, forage quality and quantity are likely more limiting for ungulate populations in the southwestern United States. During the drought of the pretreatment period, the presence of water catchments was not sufficient to prevent the high adult mortality rates we observed. Thus, providing water sources for ungulates during drought periods may do little to prevent the adverse consequences of a limited forage supply.

The relationships between precipitation and home-range size, movement rates, and mortality supports the idea that forage had a greater influence than water on desert bighorn sheep in the treatment range during this study. During periods of above-normal precipitation, high forage moisture content and abundant natural sources of freestanding water may minimize the influence of anthropogenic water catchments and during periods of severe drought, forage conditions are likely the primary limiting factor for desert bighorn sheep. Therefore, the influence of anthropogenic water catchments, if any, on desert bighorn sheep

populations may be strongest during years with weather conditions that are neither drought nor wet periods.

Our study also demonstrates the importance of long-term ecological research when studying long-lived animals that inhabit highly variable environments. Examining how these water catchments influence desert bighorn sheep allows us to better understand, conserve, and manage ecosystems and populations of large herbivores in arid environments. To adequately address the question of the influence of water catchments on desert bighorn sheep, controlled and replicated studies that are of a long enough duration to capture the range of environmental variability (i.e., drought, moderate precipitation, and high precipitation) inherent in the desert Southwest will be needed. Short-term manipulative studies on the influence of anthropogenic water sources are more susceptible to the vagaries of weather conditions during treatment and control periods (Shaw 1971). Based on the duration of this study, we suggest that future studies >10 years in duration will be necessary to adequately address this issue. In addition, any future studies should be conducted using replicated pairs of control and treatment mountain ranges. Future research on the influence of anthropogenic water sources on wildlife should have a serious long-term commitment for funding and support. Further short-term studies will likely be ineffective.

Although it would have been ideal if removal of water catchments coincided with the drought, other studies have examined how desert mule deer and desert bighorn sheep respond to addition of water catchments. Within 3 years after construction of catchments, these studies failed to detect a change in habitat use in response to addition of water sources (Krausman and Etchberger 1995, Marshal et al. 2006). Examining how these water catchments influence desert bighorn sheep allows us to better understand, conserve, and manage ecosystems and populations of large herbivores in arid environments.

Water catchments are used by a variety of other species (Cutler and Morrison 1998, Kuenzi 2001, Lynn et al. 2006, O'Brien et al. 2006). However, the influence of catchments on population performance (i.e., reproduction, recruitment, and survival) of these taxa is largely unknown. Until studies are completed, documenting the influence of water catchments on the variety of taxa that use them, the current controversy over maintenance and construction of water catchments will likely remain a political matter.

SUMMARY

Removal of water catchments in the treatment range did not result in the predicted changes in diet selection, foraging area selection, home-range size, or movement rates, mortality, productivity, or recruitment. In addition, we did not document increased mortality or a change in lamb:female or yearling:female ratios after removal of water catchments.

Browse consumption in the treatment range increased approximately 10% during early summer from pretreatment to posttreatment; we did not detect a change in grass, forb, or cacti consumption during any season. We did not document any changes in percent cover of the browse, forb, grass, or cacti in foraging areas used by desert bighorn sheep. Thermal cover in foraging areas used by desert bighorn sheep in the treatment range was higher during the summer months of posttreatment (70% during early summer and 96% during late summer) than during pretreatment.

Winter home ranges (50% and 95% home ranges) increased by 57–60% in the treatment range and declined by approximately 50% in the control range from pretreatment to posttreatment. Autumn home ranges increased by 71–88% in the treatment range from pretreatment to posttreatment. Winter movement rates in the treatment range increased by 35% and decreased in the control range by 24% from pretreatment to posttreatment. Distance to the nearest water catchment during winter decreased by 25% and 9% in the treatment and control ranges, respectively. We did not document changes in home-range area, movement rates, or distance sheep were from water during hotter months.

Most mortality occurred during summer. Mean survival rate was lower during pretreatment than during posttreatment in both mountain ranges. Annual survival rates were positively associated with precipitation. We did not find a significant decrease in lamb:female or yearling:female ratios in the treatment range due to removal of water catchments.

The lack of significant changes in diet, foraging area characteristics, movement rates, home-range size, mortality, productivity, and juvenile recruitment in response to removal of water catchments suggests that during years with above-normal precipitation, perennial sources of freestanding water may not be limiting to desert bighorn sheep in the treatment range and may have little influence during times when forage moisture content is high. Conversely, during periods of drought, forage quality and quantity are likely more limiting for ungulate populations in the southwestern United States. During the pretreatment drought, the presence of water catchments did not prevent the high adult mortality rates observed in both ranges. Therefore, providing water sources for ungulates during drought periods may do little to prevent the adverse consequences of a limited forage supply.

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Isla Pinta, Sierra Pinta Mountains, Cabeza Prieta National Wildlife Refuge, Arizona, USA.

Vegetation conditions in the Tule Desert (located between the treatment and control ranges) during the severe drought of 2002, Cabeza Prieta National Wildlife Refuge, Arizona, USA.

Vegetation conditions in the Tule Desert (located between the treatment and control ranges) during the abnormally wet period of 2005, Cabeza Prieta National Wildlife Refuge, Arizona, USA.