


RESEARCH ARTICLE



Habitat selection and water dependency of feral burros in the Mojave Desert, California, USA

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Funding information

U.S. Department of Defense

Abstract

Expansion of feral burro (*Equus asinus*) populations across the southwestern United States is causing human–wildlife conflicts including rangeland degradation, competition with livestock and native species, and burro–vehicle collisions. On the Fort Irwin National Training Center (NTC) in California, feral burros interfere with military training and are involved in vehicle collisions and other conflicts (e.g., burros blocking access to buildings). Limited data on burro movements and resource use poses a challenge for the development of management plans and mitigation strategies. We estimated home range size, second- and third-order seasonal resource selection, and water dependency of 10 adult female feral burros fitted with global positioning system (GPS) collars on the NTC from November 2015 to April 2017. Mean 95% autocorrelated kernel home range size of female burros ($253.9 \pm 30.7 \text{ km}^2$ [SE]) did not differ among seasons or between burros that resided close to or far from urban areas. Burros selected areas closer to water in all seasons and at both spatial scales, but selection was stronger in the dry season and at the landscape scale. When available, burros strongly selected for areas closer to urban areas. Burros consistently selected for areas with green forage and at lower elevations, but selection for other topographical features was variable. Water use patterns were consistent with the resource selection results. Burros visited water sources twice as often (every $22.2 \pm 6.3 \text{ hr}$) during the hot-dry season (Apr–Oct) compared to the cool-wet seasons (Nov–Mar;

2015: 45.9 ± 21.0 ; 2016: 39.7 ± 9.3 hr). Our results suggest that urban areas, and resources therein, and water sources have the biggest influence on burro resource selection, and management plans could focus mitigation programs on these areas.

KEYWORDS

Equus asinus, feral burro, human–wildlife conflict, military base, resource selection, space use, water dependency

Feral burro (*Equus asinus*) populations occur across much of the southwestern United States. Recent population estimates on lands managed by the Bureau of Land Management (BLM) exceed 17,000 burros (BLM 2022a). Feral burro populations can have an average annual growth rate up to 19% per year (Ransom et al. 2016). Feral burro populations in California on BLM lands exceeded appropriate management levels by 55% in 2021 (BLM 2022a, b). Population estimates derived from surveys on herd management areas (HMA) underestimate the number of feral burros in the Southwest because they largely omit burros occurring outside of HMAs on lands that are managed by other agencies (e.g., National Park Service, Department of Defense). For example, the feral burro population on Fort Irwin National Training Center (NTC), California, was recently estimated at 690 burros based on partial surveys in 2016 and 2017, but these burros are not included in estimates for BLM HMAs in California, which were 3,391–3,657 burros during the same period (Gedir et al. 2021, BLM 2022b).

Overabundant feral burro populations can degrade rangelands, compete with native ungulates, and cause human–burro conflict (Sanchez 1974, Longshore and Douglas 1988, Abella 2008, National Research Council 2013). Overgrazing by burros can alter vegetation structure and plant community composition (Sanchez 1974, Weaver 1974, Hanley and Brady 1977) and lower stocking rates of rangelands (Scasta et al. 2018), which is exacerbated in arid areas (Dave 2010). During periods with limited forage availability, feral burros may compete for forage with desert bighorn sheep (*Ovis canadensis nelsoni*) and mule deer (*Odocoileus hemionus*; Marshal et al. 2008, 2012). The presence of threatened desert tortoise (*Gopherus agassizii*) in the Sonoran Desert was negatively associated with feral burros, with the burros damaging critical habitat and reducing forage for tortoises (Berry et al. 2020). In arid systems, burros trample vegetation and compact soil near limited perennial water sources (Tiller 1997, Beever et al. 2008, Ostermann-Kelm et al. 2009), which can also reduce flow rates of springs and contribute to their drying (Weaver 1974). Feral equids can also interfere with the use of water sources by native ungulates (Dunn and Douglas 1982, Ostermann-Kelm et al. 2008, Hall et al. 2018). In more populated areas, burros cause vehicle collisions resulting in personal injury and property damage (Cramer and McGinty 2018), and their presence on military bases can interrupt or delay multimillion-dollar training exercises (Perryman and Muchlinski 1987, Tiller 1997). Feral burros may also provide an ecological benefit in some contexts. According to Lundgren et al. (2021), well digging by feral burros in desert washes near perennial springs or in streams with subsurface flow increased local availability of drinking water for other wildlife species and enhanced germination of some riparian plants. Species richness and visit duration at water wells dug by burros did not differ from background waters (i.e., available water present in the absence of burro digging), but background waters had higher visitation frequency by other species. At one site, surface water was limited to burro wells when background water dried during the course of the season. Lundgren et al. (2021) concluded that feral burros could be viewed as an unintentional rewilding that may replace ecological functions lost when native equids went extinct in the late Pleistocene. Other researchers, however, suggested that Lundgren et al. (2021) largely ignored the broader net-negative environmental effects of feral burros in the Southwest (Bleich et al. 2021, Rubin et al. 2021). Further, there has been a shift in climate and vegetation across much of the southwestern United States from one of mesic woodlands and grasslands, with numerous perennial lakes in the Pleistocene to the water-limited, arid deserts present today (van Devender and King 1971, King 1976, van Devender and Spaulding 1979, Thorne 1986).

When domestic livestock or native wild ungulates become overabundant, managers can reduce stocking rates for livestock or increase hunter harvest of native ungulates to mitigate negative environmental effects and human–wildlife conflicts. But many feral burro populations are protected under the Wild Free-Roaming Horse and Burro Act of 1971 (WFRHBA; Public Law 92-195), which limits options for population control. Burros in the HMAs and herd areas (HAs) created when the Act was passed in 1971 are under the full protection of the Act. Other burro populations that reside outside of HMAs and HAs, such as those on Department of Defense lands, are not covered under the WFRHBA. Although not specifically prohibited by the WFRHBA, subsequent congressional actions prohibit lethal population control of burros covered under the WFRHBA (i.e., in an HMA) except in extreme situations (e.g., sick, injured). The BLM currently traps and moves burros to off-range holding facilities and makes them available to the public for adoption. Capturing and adopting out burros in long-term holding facilities is not a sustainable approach to management of these populations (Scasta et al. 2018). Thus, other means of population control need to be explored.

One potential management option that has public support is fertility control using immunocontraceptives, which cause the immune system to prevent pregnancy (National Research Council 2013). The logistics of an effective immunocontraceptive program are challenging for large, free-ranging populations (Kirkpatrick et al. 2011, Gedir et al. 2021). Popular immunocontraceptive compounds (such as Porcine Zona Pellucida; PZP) that have been approved for use need to be administered annually, resulting in the need for multi-year identification of individual animals (Kirkpatrick et al. 2011, National Research Council 2013). Immunocontraceptives are most often administered by darting free-ranging animals, trapping, or roundups. Fertility control programs using immunocontraceptives are unlikely to result in substantial reductions in population growth unless a large segment of the female population is treated, particularly for immunocontraceptives requiring multiple doses (Gedir et al. 2021).

Relative to other large ungulates, feral burros have been the subject of comparatively few studies examining their resource selection and movements, particularly since the development of global positioning system (GPS) collars. Burros are adapted to arid climates but rely on water for thermoregulation and other physiological mechanisms (Maloiy 1970, Woodward 1979, Moehlman 1998, Zakari et al. 2015). Burros must ingest more water than arid-adapted ruminants (adjusting for body size) because of their hind gut fermentation, production of large amounts of feces with high moisture content, and comparatively low urine concentrating ability (i.e., high fecal and urinary water loss; Joubert and Louw 1976, Maloiy et al. 1979, Cain et al. 2012, Kihwele et al. 2020, Esmaeili et al. 2021). As a result, burros are commonly found close to water sources and visit water sources more frequently during hot-dry periods (Seegmiller and Ohmart 1981, Kaczensky et al. 2010, Giotto et al. 2015). Burros have a flexible diet that changes seasonally based on forage availability. When available, forbs and grasses make up a large part of their diet, but burros will consume significant amounts of browse when the availability or nutritional quality of grasses and forbs decline (Abella 2008, Hamrick et al. 2015, Malo et al. 2016). Behavioral thermoregulation strategies and habitat selection vary across diel and seasonal cycles in arid climates. Burros use shade from topographic features and vegetation cover to reduce heat loads during summer and as thermal cover from the wind (Woodward and Ohmart 1976, Giotto et al. 2015). For example, burros select steeper slopes and vegetated washes during the day, and flatter slopes during the night in summer, but during cool periods, burros remain on flatter slopes during the day and then select for steeper slopes and washes during the night (Woodward and Ohmart 1976, Giotto et al. 2015).

We sought to examine water dependency and habitat selection of feral burros, in part, to determine if patterns in habitat selection and water use would facilitate fertility control efforts by identifying areas of the landscape or point resources frequented by feral burros, where trapping efforts or darting could be used to administer immunocontraceptives. Our objectives were to estimate home range size, assess resource selection, and estimate the frequency of seasonal water use of feral burros at Fort Irwin NTC in the Mojave Desert of California. Feral burros on the NTC are not protected by the WFRHBA; thus, the Department of Defense has more options available to manage feral burros than does BLM when managing burros on HMAs. To prevent public outcry, the use of lethal removal was not seriously considered by base authorities at the time of our study. While burros can be captured on

base, trapping can only happen on certain areas on base owing to military activities (e.g., bombing ranges with unexploded ordnance). Thus, a more long-term management option was needed.

We expected that burro habitat selection would be primarily influenced by water dependency, forage characteristics, and thermoregulatory constraints, particularly during the hot-dry season. Dependency on water would result in smaller home ranges during the hot-dry season compared to the cool-wet season. Because urban areas provide multiple resources (i.e., multiple sources of forage, water, and thermal cover) in a small area, we predicted that burros would select for areas closer to urban environs when available and that selection for urban areas would be stronger in the dry season. We also expected that burros using urban areas would have smaller home ranges in association with concentrated forage and water resources. In all seasons, we expected burros to select slopes with north-facing aspects and areas closer to washes because of the potential for higher forage quality and thermal cover in these areas and we expected that burro use of topographic features such as slope and elevation would be based on avoiding thermal stress and use of those features would vary by season and time of day.

STUDY AREA

Fort Irwin NTC is a military base located in the Mojave Desert approximately 60 km northeast of Barstow, California (Figure 1). China Lake Naval Air Weapons Station and Death Valley National Park are just northwest and north of the NCT, respectively. The NTC encompasses 3,055 km² and is divided into 3 main regions: the garrison, National

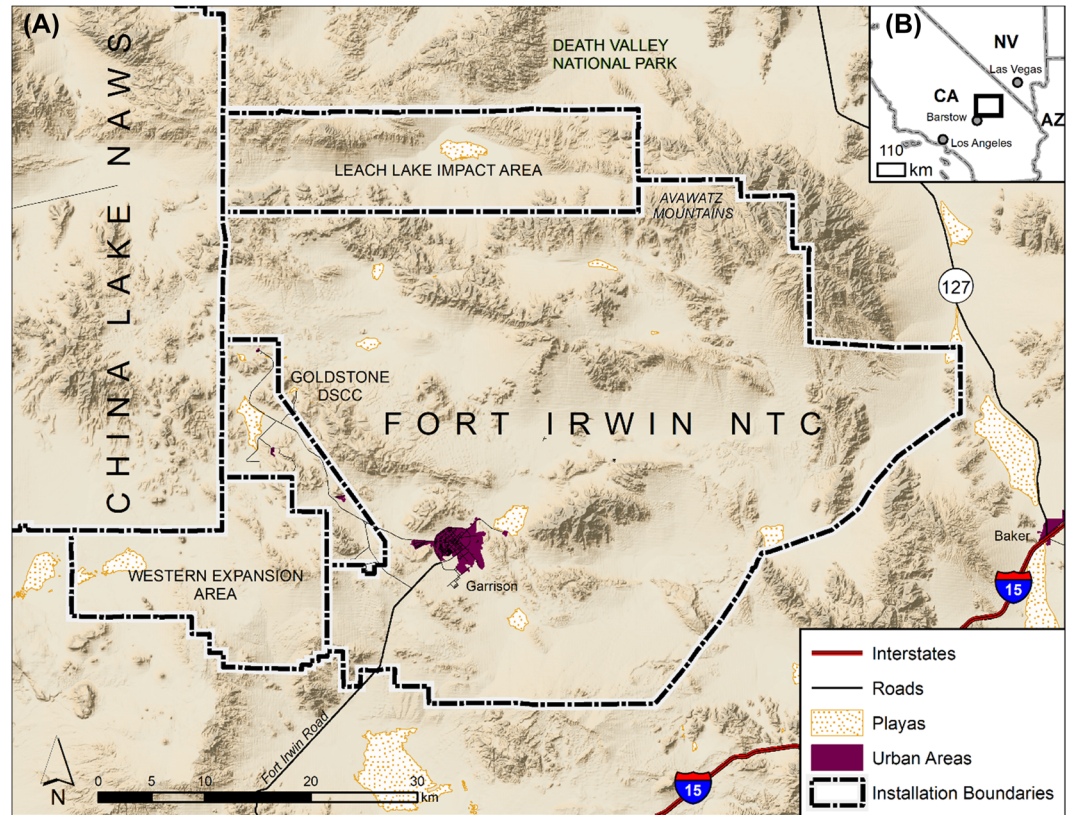


FIGURE 1 Location and topography of the Fort Irwin National Training Center in California, USA, where feral burros were tracked from November 2015 to April 2017.

Aeronautics and Space Administration Goldstone Deep Space Communication Complex (Goldstone Complex), and down-range training areas (i.e., down range). The garrison covers 18 km² and is highly developed with a population of >8,000 people. Resources for burros in the garrison include thermal cover, irrigated vegetation, sewage treatment ponds, and other water sources. West of the garrison is the Goldstone Complex, which has 3 active antenna sites with associated outbuildings and landscaping, which are used by burros for thermal cover, forage, and water. Two large playas provide an ephemeral source of water after rains, but there are no known perennial springs on the Goldstone Complex. North and west of the garrison are the down-range training areas. The Western Expansion Area is relatively undisturbed by training exercises but is generally lacking perennial water. Portions of the down-range training areas are highly disturbed from training activities, but other areas are typical of the relatively undisturbed Mojave Desert. In the down-range area, 8 springs have water for at least part of the year, and multiple playas retain rainwater in the wet season and temporarily after summer rains. All branches of the military train on the base in a rotational bi-weekly on range-off range schedule. There are model cities and targets for training, many of which are used as thermal cover by burros.

The terrain is composed of rugged desert mountain ranges surrounded by alluvial valleys; elevation ranges from 145 m to 1,875 m. Predominant vegetation types include Sonora-Mojave creosote bush-white bursage (*Larrea tridentata*-*Ambrosia dumosa*) and Mojave mid-elevation mixed desert scrub (blackbrush [*Coleogyne ramosissima*], California buckwheat [*Eriogonum fasciculatum*], and Nevada ephedra [*Ephedra nevadensis*]). While bighorn sheep were documented at springs on the base using trail cameras, other large mammals such as mule deer and mountain lions (*Puma concolor*) were not observed (J. W. Cain, New Mexico State University, unpublished data). Long-term (1948–2015) average annual precipitation is 94.2 ± 49.8 mm (SD); 59% of which occurs from November to March (Daggett Federal Aviation Administration Airport; Western Regional Climate Center 2016). Average daily high and low temperatures range from 40°C to 22°C in July and from 15°C to 1°C in December. Mean monthly maximum temperatures are 33.9°C and 18.9°C from April through October and November through March, respectively. Because of differences in precipitation and temperature by year, we divided the study period into 1 hot-dry season (Apr–Oct 2016) and 2 cool-wet seasons (Nov 2015–Mar 2016 and Nov 2016 to Mar 2017; Western Regional Climate Center 2016).

METHODS

Capture and handling

We captured feral burros using 2 methods: corral traps and darting from a vehicle. We baited corral traps with alfalfa hay, carrots, apples, and water and checked traps at least twice a day. We transferred captured burros by trailer to a temporary holding pen on the NTC where we fed and watered them daily and held them for no more than 1 week. We then transported these burros to the BLM Wild Horse and Burro Facility located in Ridgecrest, California, where they were held until processed (approximately 2–3 weeks). Although BLM does not have management oversight over burros on the NTC, they provided advice and support with burro trapping as part of interagency cooperation with the NTC. We also darted burros from a truck using 0.012–0.016 mg/kg etorphine hydrochloride and 0.8 mg/kg xylazine, reversed with 0.6–0.8 mg/kg of naltrexone and 1.6 mg/kg of tolazoline. We marked, collared, and released these burros at the point of capture.

We freeze-branded a unique ID number on each side of the rump of all burros using liquid nitrogen and numbered irons (Householder et al. 1999) and collected morphological measurements and blood samples. We aged burros using tooth eruption and wear patterns and a licensed veterinarian assessed pregnancy status using a portable ultrasound. We released all corral-trapped burros near the point of capture. We processed and handled burros darted in the field in a similar manner except that we did not age them and the ultrasound was not available. We fitted 10 adult females with GPS collars programmed with a 1-hour fix interval (Telonics TGW-4500-3, store on board, Mesa, AZ, USA). Additional details on burro captures are provided in Karish (2020).

Home range estimation and resource selection

We estimated minimum convex polygons (MCP) and kernel home ranges to delineate areas appropriate for resource selection analyses and to explore patterns of space use, respectively. Despite their known disadvantages, we estimated MCP home ranges because it allowed a general comparison of burro home range size in our study with previously published home range estimates from across the Southwest. We also used MCPs to delineate available areas for resource selection analyses as described below. In addition, we estimated seasonal home range size using kernel density estimators. We used the Adehabitat (Calenge 2006) and CTMM (Fleming and Calabrese 2021) packages in program R (R Core Team 2019) to estimate seasonal 95% MCPs, and autocorrelated 95% kernel home ranges and 50% kernel density core areas for each GPS-collared female. After calculating seasonal home range and core use areas, we classified collared burros into 2 types: close-range burros, which we defined as those burros with urban areas available in their home ranges, and down-range burros, which had home ranges primarily in the down-range training areas and did not have access to urban areas. We made this distinction because we expected that the proximity to urban areas may influence home range size and habitat selection. We assessed the proximity of MCP home ranges and urban areas seasonally for all study animals and burros never changed between close and down range. We used repeated measures analysis of variance (ANOVA) in program R to determine if 95% MCP home ranges, 95% kernel home ranges, and 50% core areas differed by season and burro type (R Core Team 2019). Prior to analysis, we tested data for normality and homogeneity of variance using Shapiro-Wilk and Levene's tests; our data met the assumptions.

Burros have a fission-fusion social structure where no permanent bonds exist between adult individuals and the only stable group is a female and her offspring (Moehlman 1998). Some individual collared burros occasionally moved together in the same herd, but herd membership was highly variable and changed frequently. We grouped collared animals into herds during periods when individuals spent >24 hours within 400 m of each other; otherwise, we considered burros to be independent. We obtained the 400-m cut-off for defining herd membership by assessing the movements of each GPS-collared burro in relation to every other collared animal. If the distance was >400 m between 2 burros, the burros moved independently 97.7% of the time ($n = 30,640$); if the distance was <400 m between burros, they moved together 98.3% of the time ($n = 42,412$). During periods when collared burros were together, we represented that herd in the data set with locations from only 1 collared animal to avoid pseudoreplication.

To define the available areas for resource selection, we created seasonal MCPs for each collared female (third-order selection) using Geospatial Modelling Environment (Beyer 2012), then buffered the seasonal MCPs by 400 m based on the mean maximum hourly movement rate (389.0 ± 30.5 m). For second-order selection, we defined the available area based on a 100% MCP estimated seasonally from all combined burro locations collected throughout the entire study buffered by the mean maximum hourly movement rate (400 m). We then generated 2 random points for every burro location within the landscape-scale MCP and the individual herd home ranges to assess second- and third-order habitat selection, respectively (Johnson 1980, Marshal et al. 2004).

We sought to identify potential resources that might be targeted for manipulation (e.g., fencing, habitat manipulations) to reduce burro conflicts on the NTC or those that might contribute to the development of a more effective fertility control program. Habitat characteristics included vegetation cover type, forage conditions, elevation, slope, aspect, distance to washes, distance to the nearest urban area, thermal cover, and water sources. We extracted estimates of all habitat characteristics for used and available locations. We included 2 predictor variables related to forage conditions: vegetation type and normalized difference vegetation index (NDVI). We obtained vegetation type from the LANDFIRE website at 30-m resolution (LANDFIRE 2014) and reclassified these into 6 vegetation types (playa <2% of the landscape; creosote bush-white bursage = 38.9%, mid-elevation mixed desert scrub = 15.5%, sparsely vegetated = 33.4%, barren = 10.4%, and urban <1% of the landscape; Table S1, available in Supporting Information). Abundance of forage species preferred by burros can vary across vegetation types, whereas NDVI is related to spatiotemporal variation in vegetation greenness, biomass, and photosynthetic

activity. We calculated NDVI at the 250-m resolution from the raw 8-day time step reflectance data obtained from the moderate resolution imaging spectroradiometer (MODIS) on the Aqua and Terra satellites (Vermote 2015). We then calculated the NDVI rate of change (Δ NDVI) for each pixel over the study period by taking the difference in NDVI between 2 consecutive 8-day periods using the raster calculator in ArcGIS 10.3 (Esri, Redlands, CA, USA). We extracted the time-specific NDVI and Δ NDVI values by matching the date of a known location to an appropriate date range of the MODIS images (Marshall et al. 2004). A high NDVI value would indicate greener, denser vegetation and a positive Δ NDVI value indicates that an area is greener than it was in the previous time step (i.e., the area would be greening up with new plant growth). We expected burros to select areas with more vegetation biomass, greener forage, and areas that were increasing in forage quality (i.e., positive Δ NDVI).

Slope and elevation influence burro habitat selection with effects varying with season and available forage (Woodward and Ohmart 1976, Marshall et al. 2012). We also expected aspect to affect selection because north-facing slopes typically have lower solar exposure, are often more shaded, and have higher soil moisture, resulting in higher vegetation biomass (in the northern hemisphere). Use of north-facing slopes may minimize heat loads during summer (Gedir et al. 2020). We used a 10 × 10-m digital elevation model (DEM) to estimate percent slope and aspect in ArcGIS (U.S. Geological Survey [USGS] 2023). We used the cosine function to convert aspect to a noncircular, continuous variable representing northness with values closer to -1 representing south-facing aspects and values closer to 1 representing north-facing aspects (Nussear et al. 2009).

Washes in arid areas provide thermal cover for burros and provide greener vegetation longer into the dry season because of increased soil moisture from rainwater runoff (Woodward and Ohmart 1976, Giotto et al. 2015). We used the National Hydrography Dataset (USGS 2023) to identify the location of washes and calculated the distance from each used and random location to the nearest wash. We identified the location of perennial water sources with preexisting geographic information system (GIS) data collected by the NTC Integrated Training Area Management team, which included springs, water treatment ponds, and irrigation ditches. To determine extended periods of ephemeral water availability in natural playas, we used band 6 from 16-day interval Landsat 8 satellite data at 30-m resolution (Weinberg et al. 2015). We compared each sequential image to establish when each playa was inundated with water. To determine which day within the 16-day interval a playa filled, we used daily precipitation records from weather stations on the NTC. Using rainfall measured daily, we were able to estimate when playas likely flooded or refilled and then adjusted the extent of the water coverage of the playa in ArcGIS. If a playa was dry in 1 16-day image and water was present in the subsequent image, but there was no rainfall recorded at weather stations in that time period, we assumed that it became inundated at the midpoint of the 2 images. The locations of playas were included in our calculation of the distance to the nearest water sources and applied to all used and available points during periods when water was available in each playa in second- and third-order habitat selection.

Urban areas, the garrison, and the Goldstone Complex have associated anthropogenic water sources, green forage (e.g., watered lawns, landscaping), and structures that provide thermal cover (e.g., buildings, trees, other structures). We also updated existing data on the location of human structures that occurred down range by digitizing recently constructed buildings and targets. These structures provide thermal cover for burros in areas where shade was otherwise sparse. We then measured the distance from each used and random location to the nearest urban area or structure.

We expected that urban areas could have a potentially large effect on burro habitat selection, but they were not available to all collared burros. To account for this difference in availability, we classified each burro herd by burro type as either close-range burros or down-range burros as previously described. We then used the burro type as a predictor variable in interaction terms with other habitat characteristics (i.e., distance to water, NDVI) when we thought the influence of those habitat characteristics would vary depending on whether or not burros had urban resources available within their home range. The primary interest here was to determine the influence of urban areas on habitat selection of burros with home ranges near urban areas.

Burros have consistent diel behavioral patterns of foraging and drinking (Xia et al. 2013, Zakari et al. 2013, Giotto et al. 2015). In hot, arid climates, diel activity patterns can shift during hot months (Cain et al. 2006, Zakari et al. 2013).

Nocturnal foraging by burros increases during summer compared to winter (Woodward and Ohmart 1976). Habitat selection is often related to the behavioral state of the animal, and thus can change across diel periods. Because of the extreme temperatures during the hot-dry season, we predicted burro habitat selection would be partially determined by an avoidance of areas with high daytime thermal loads. Therefore, we classified locations into 3 diel time periods: crepuscular, day, and night. We considered morning crepuscular period to commence at civil twilight and end 4 hours later, day was from the end of the morning period until the start of the evening crepuscular period, and the evening crepuscular period started 4 hours before and ended at civil twilight. Night was the period between civil twilight in the evening and civil twilight in the morning. We adjusted civil twilight biweekly and estimated times to the nearest quarter hour (U.S. Naval Observatory Astronomical Applications Department 2015). We combined the morning and evening crepuscular periods because previous studies reported burro activity patterns to be similar during these periods (Xia et al. 2013, Zakari et al. 2013, Giotto et al. 2015).

Resource selection analysis

Prior to analysis, we tested all predictor variables for multicollinearity and did not include correlated variables with an $|r| > 0.60$ in the same model (Table S2, available in Supporting Information). We standardized all continuous variables using a z-score, allowing us to compare the magnitude of parameter estimates within seasonal models sets for resource selection analyses. We then created 42 *a priori* models to assess resource selection by feral burros, including single-variable models (Table S3, available in Supporting Information). We used mixed-effects logistic regression to model second- and third-order habitat selection using the lme4 package in program R (Bates et al. 2015, R Core Team 2019) with burro or herd ID included as a random intercept (Gillies et al. 2006). We used the crepuscular period as the reference level for the diel period and creosote bush-white bursage as the reference level for vegetation type. In the model set, we developed models that contained only main effects and those including biologically relevant interaction terms. To account for our predictions that both diel period and the availability of urban areas would influence burro habitat selection, we included both as interaction terms with other habitat covariates (i.e., slope, elevation, distance to urban, distance to thermal cover, and distance to water) that could plausibly have a different influence on selection depending on the time of day or availability of urban areas. We evaluated all models for each season and at each spatial scale. We also calculated variance inflation factors to evaluate multicollinearity between multiple variables within the models. We eliminated any models with an inflation factor of ≥ 5.0 from further consideration (Menard 2002).

We used Akaike's Information Criterion corrected for small sample size (AIC_c) to rank models and assess model support (Burnham and Anderson 2002). We considered any models with a $\Delta AIC_c \leq 2$ to be competing models but considered models with ΔAIC_c from 2 to 7 to have some support. We then evaluated the performance of each of the highest-ranking seasonal models using *k*-fold cross-validation (Boyce et al. 2002) in Program R (R Core Team 2019).

Water dependency

To evaluate the water dependency of burros, we estimated the seasonal distribution of female feral burros around water sources based on GPS collar data and the seasonal frequency, timing, and duration of water use. Initially, we identified dates when burros potentially visited water sources by identifying all GPS positions for each burro that were within 400 m (i.e., average hourly burro movement) of a water source. We then used the tracking analyst extension in ArcGIS to plot the daily movement paths connecting all consecutive GPS locations for each burro (Cain et al. 2012). Movements to water sources were characterized by a clear trajectory toward a water source, followed by a return movement trajectory. When the trajectory of a burro movement path ended at a water source, we included only locations at the water source as a visit and used the last location at the water source during each visit to calculate water use frequency. If the trajectory ended before the water source, we counted the point closest to

the water source as the visit. We calculated the time between visits from the time of the last location of the visit until the time of the first location of the next visit. To estimate the duration of water visits, we took a more conservative approach and summed the number of consecutive GPS locations for individual burros that were within 100 m of a perennial water source by dates corresponding to those identified above as water visits based on movement trajectories and proximity to perennial water.

We then used repeated measures ANOVA to compare the time between visits to the water source for burros between seasons, and burro types, to compare the mean distance from GPS telemetry locations to water sources between seasons and burro types, and to compare the mean duration of water visits by season and burro type. The within-subjects factors were season and burro type (close range, down range) and the individual burros were the subjects. Prior to analysis, we tested data for normality and homogeneity of variance using Shapiro-Wilk and Levene's tests; our data met the assumptions.

RESULTS

We captured and collared 10 adult females; 6 were captured via corral traps and 4 by darting. Six of the GPS-collared burros were with foals when they were captured (2 of the darted burros and 4 of the corral-trapped burros). Four of the corral-trapped animals were pregnant. For those burros that we darted from a vehicle (including burros fitted with very high frequency [VHF] collars not reported in this manuscript; Karish 2020), the time between darting and immobilization (recumbent with head down) ranged between 3 and 17 minutes (mean = 6.4 min \pm 4.7 min [SD], median = 4 min; $n = 9$) and the time between administering the reversal and the time the burro ran away ranged between 1 and 3 minutes (mean = 1.8 min \pm 0.9 min [SD], median = 1.5 min, $n = 8$). We had no capture-related mortalities or post-capture myopathy of any darted or corral-trapped burros.

Home ranges

We were able to collect data from 10 GPS-collared female burros from November 2015 until April 2017. All 10 GPS-collared burros survived the entire study, so the sample size was the same for each season. Seven burros had home ranges that overlapped urban areas and were classified as close-range burros and 3 burros were down range and never had access to urban areas or the resources therein. The GPS collars had a mean fix rate of 99% (SD = 2.5%), resulting in 123,430 GPS locations. Seasonal 95% MCP home ranges for these females ranged from 25 km² to >430 km² (Table 1). Mean (\pm SE) MCP home range size was 157.02 \pm 46.6 km², 142.2 \pm 20.3 km², and 198.3 \pm 42.3 km² for the 2015 cool-wet season, 2016 hot-dry season, and 2016 cool-wet season, respectively. Mean (\pm SE) 95% autocorrelated kernel home range size was 235.1 \pm 60.1 km², 220.5 \pm 40.5 km², and 306.1 \pm 58.5 km² for these same seasons (Figure S1, available in Supporting Information), respectively. Mean 50% kernel core area was 67.0 \pm 24.1 km², 51.1 \pm 9.4 km², and 70.8 \pm 13.5 km² for the 2015 cool-wet season, 2016 hot-dry season, and 2016 cool-wet season, respectively (Table 1). There were no differences in the size of the 95% MCP home ranges ($F_{2,16} = 0.676$, $P = 0.523$), 95% kernel home ranges ($F_{2,16} = 818$, $P = 0.459$), and 50% core areas ($F_{2,16} = 10.425$, $P = 0.661$) between seasons. There was weak evidence for differences in home range size between close-range and down-range burros (burro type) for 95% MCP home ranges ($F_{1,16} = 3.44$, $P = 0.082$), but home range size did not differ between the types for 95% kernel home ranges ($F_{1,16} = 609$, $P = 0.458$) or the 50% core areas ($F_{1,16} = 0.687$, $P = 0.431$). Mean (\pm SE) size of MCP (close-range burros 191.0 \pm 28.6 km² vs. down-range burros 108.1 \pm 18.4 km²), 95% kernel home ranges (close-range burros 271.6 \pm 37.7 km² vs. down-range burros 212.3 \pm 53.0 km²), and 50% core area (close-range burros 68.9 \pm 12.5 km² vs. down-range burros 49.1 \pm 12.3 km²) were larger for close-range burros than down-range burros. There was no interaction between burro type and season for the 95% MCP ($F_{2,16} = 0.038$, $P = 0.963$), 95% kernel home ranges ($F_{2,16} = 1.108$, $P = 0.354$), or 50% core areas ($F_{2,16} = 0.726$, $P = 0.499$; Table 1).

TABLE 1 Seasonal home range estimates (km²) for adult global positioning system-collared female feral burros on the Fort Irwin National Training Center, California, USA, 2015–2017. Home range estimates include 95% minimum convex polygon (MCP), 95% autocorrelated kernel home ranges, and 50% core areas.

Burro ID	Home range						Core area		
	95% MCP (km ²)			95% kernel estimate (km ²)			50% kernel estimate (km ²)		
	2015 cool-wet	2016 hot-dry	2016 cool-wet	2015 cool-wet	2016 hot-dry	2016 cool-wet	2015 cool-wet	2016 hot-dry	2016 cool-wet
4	416.8	172.2	265.7	584.9	293.4	370.7	261.5	67.9	85.8
5	433.6	179.9	285.7	513.4	292.2	369.4	118.8	67.6	85.5
6	134.6	174.5	389.2	195.9	250.6	452.9	45.3	58.0	104.8
26	38.9	97.7	25.0	37.2	152.3	27.0	8.6	35.2	6.3
28	100.3	95.1	413.6	146.4	99.7	556	33.9	23.1	128.7
31	138.0	208.7	99.0	261.1	381.8	130.5	60.4	88.3	30.2
40 ^a	28.7	174.6	156.8	32.3	181.1	276.2	7.5	41.9	63.9
41	46.7	221.8	65.7	66.9	422.4	100.5	15.5	97.7	23.3
42 ^a	142.3	35.4	150.1	205.8	45.2	230.5	47.6	10.5	53.3
59 ^a	90.3	61.7	132.1	307.4	85.9	546.7	71.1	19.9	126.5

^aDown-range burros.

Landscape-scale resource selection

There was little model selection uncertainty for habitat selection at the landscape scale (seasonal composite MCPs ranged from 1,700–2,129 km²); all seasonal model sets had a top model with essentially all the model weight (Table S4, available in Supporting Information). All top models performed well in *k*-fold cross-validation (all *p* ≥ 0.95). The most supported models had the same structure during the 2015 and 2016 cool-wet seasons (Table S4). Burros selected lower elevations, areas with higher NDVI, and lower ΔNDVI (Table 2). Burro use of slopes differed between the 2 cool-wet seasons with burros selecting for steeper slopes in 2015 but flatter slopes in 2016 (Table 2). Burros selected for areas closer to washes during the 2016 cool-wet season, whereas confidence intervals for the parameter estimate encompassed 0 during the 2015 cool-wet season (Table 2). Close-range burros showed strong selection for areas closer to urban areas (Table 2; Figure 2). Distance to water had a strong influence on landscape-scale habitat selection for all burros, but its influence was greater for close-range burros (Figure 3).

During the hot-dry season, burros selected for lower elevation, flatter slopes, lower rates of ΔNDVI, and areas closer to water and washes (Table 2). The influence of NDVI on the relative probability of use of down-range burros was slight; however, the relative probability of use for close-range burros increased dramatically with increases in NDVI (Figure S2, available in Supporting Information). The close-range burros selected strongly for areas closer to urban areas (Figure 2).

Within home range resource selection

There was little model selection uncertainty for habitat selection at the within home range scale (i.e., third-order selection); all seasonal model sets had a top model with essentially all the model weight (Table S5, available in Supporting Information) and performed well in *k*-fold cross-validation (all *p* ≥ 0.95). Model structure for the highest-ranking model differed across seasons (Table S5).

TABLE 2 Parameter estimates, standard errors, lower and upper 95% confidence limits, z-scores, and *P*-values for variables in the highest-ranking seasonal models for landscape-scale habitat selection by global positioning system-collared female feral burros on the Fort Irwin National Training Center, California, USA, 2015–2017.

Variable ^a	β	SE	95% CI		z	P
			Lower	Upper		
2015 cool-wet season						
(Intercept)	-1.89	0.14	-2.15	-1.62	-13.96	<0.001
Water	-1.01	0.02	-1.05	-0.97	-53.32	<0.001
NDVI	0.88	0.01	0.86	0.91	68.89	<0.001
Elevation	-0.95	0.02	-0.98	-0.92	-64.12	<0.001
Slope	0.07	0.01	0.04	0.09	5.50	<0.001
Urban	-1.87	0.02	-1.91	-1.83	-85.75	<0.001
Wash	-0.01	0.01	-0.02	0.02	-0.46	0.644
Δ NDVI	-0.08	0.01	-0.10	-0.07	-9.64	<0.001
Down-range	-2.17	0.25	-2.66	-1.68	-8.69	<0.001
Urban:down-range	3.61	0.04	3.53	3.68	95.43	<0.001
Water:down-range	-1.43	0.05	-1.52	-1.34	-31.00	<0.001
2016 hot-dry season						
(Intercept)	-2.50	0.11	-2.72	-2.28	-22.00	<0.001
Water	-2.15	0.02	-2.19	-2.11	-109.05	<0.001
NDVI	0.88	0.03	0.82	0.94	28.44	<0.001
Elevation	-0.50	0.02	-0.53	-0.47	-32.58	<0.001
Slope	-0.17	0.01	-0.20	-0.15	-13.41	<0.001
Urban	-2.34	0.03	-2.40	-2.29	-80.30	<0.001
Wash	-0.06	0.01	-0.08	-0.04	-5.30	<0.001
Δ NDVI	-0.09	0.02	-0.12	-0.05	-5.00	<0.001
Down-range	-1.62	0.21	-2.03	-1.22	-7.81	<0.001
Urban:down-range	5.01	0.04	4.92	5.09	113.03	<0.001
NDVI:down-range	-1.19	0.06	-1.29	-1.08	-21.61	<0.001
2016 cool-wet season						
(Intercept)	-2.80	0.15	-3.09	-2.51	-18.97	<0.001
Water	-1.06	0.02	-1.10	-1.01	-46.97	<0.001
NDVI	0.26	0.01	0.24	0.28	23.65	<0.001
Elevation	-0.25	0.02	-0.28	-0.22	-16.26	<0.001
Slope	-0.05	0.01	-0.07	-0.02	-3.75	<0.001
Urban	-2.79	0.04	-2.86	-2.72	-80.26	<0.001
Wash	-0.09	0.01	-0.11	-0.07	-8.07	<0.001
Δ NDVI	-0.03	0.01	-0.05	-0.01	-2.88	0.004

(Continues)

TABLE 2 (Continued)

Variable ^a	β	SE	95% CI		z	P
			Lower	Upper		
Down-range	-1.16	0.27	-1.69	-0.63	-4.26	<0.001
Urban:down-range	5.51	0.05	5.41	5.61	107.72	<0.001
Water:down-range	-0.96	0.04	-1.04	-0.87	-22.09	<0.001

^aUrban = distance to urban area (m). Wash = distance to nearest wash (m). Water = distance to nearest water (m). NDVI = normalized difference vegetation index. Δ NDVI = change in NDVI. Down-range indicates the effect of burro type (close-range burros were the reference level).

During the 2015 cool-wet season, burros selected for areas closer to water, at lower elevation, with higher NDVI values and lower Δ NDVI (Table 3). Confidence intervals for the parameter estimate for the influence of distance to wash included 0. The relative probability of use for down-range burros increased with increasing slope but decreased for close-range burros (Figure S3, available in Supporting Information). Close-range burros selected for areas near urban environs (Table 3; Figure 2).

During the 2016 hot-dry season, burros selected for areas closer to washes, lower elevation, flatter slopes, higher NDVI values, and lower Δ NDVI (Table 3). Close-range burros selected for areas near urban areas and both burro types had a very strong selection for water sources, with the close-range burros showing a higher relative probability of use (Table 3; Figure 3).

During the 2016 cool-wet season, burros selected for areas closer to water and washes, and also selected areas with more southern aspects and lower elevation (Table 3). Burros selected for creosote bush-white bursage compared to all other vegetation types (Table 3). The close-range burros had a steeper decline in the relative probability of use with increasing slope, whereas down-range burros selected for steeper slopes during the day, and both burro types selected for flatter slopes during the night (Figure S4, available in Supporting Information).

Water dependency

The mean distance of burros from water sources did not differ by season ($F_{2,16} = 1.76$, $P = 0.203$) or burro type ($F_{2,16} = 0.643$, $P = 0.446$), but there was evidence of a season \times burro type interaction ($F_{2,16} = 3.83$, $P = 0.044$), with down-range burros located closer to water sources during the cool-wet season in 2015. Mean distance from water sources to GPS positions collected on close-range burros was 3,617 m (95% CI = 2,912–4,322 m), 2,442 m (95% CI = 1,737–3,148 m), and 2,890 m (95% CI = 2,185–3,596 m) during the 2015 cool-wet, 2016 hot-dry, and 2016 cool-wet seasons, respectively. Mean distance from down-range burros to water sources was 2,180 (95% CI = 1,104–3,258 m) in the 2015 cool-wet season, 2,779 m (95% CI = 1,701–3,856 m) during the 2016 hot-dry season, and 2,768 (95% CI = 1,691–3,845) during the 2016 cool-wet season. The mean distance of burros to water was generally consistent across the day for all 3 seasons (Figure 4).

For both close-range and down-range burros, visits to water sources were most prevalent during the daytime (1000 to 1800) and at night (2100 to 0500), with fewer visits to water documented during the morning (0500 to 1000) and evening periods (1800 to 2000; Figures S5, S6, available in Supporting Information). Burros visited water on average every 45.9 ± 21.0 hours during the 2015 cool-wet season, every 39.7 ± 9.3 hours during the 2016 cool-wet season, and every 22.2 ± 6.3 hours during the 2016 hot-dry season (Figure 5). Burros used water 21% and 16% more frequently during the 2016 hot-dry season than during the 2015 and 2016 cool-wet seasons, respectively. Mean frequency of water use differed across seasons ($F_{2,16} = 4.66$, $P = 0.026$), but not by burro type ($F_{2,16} = 2.52$, $P = 0.151$) and there was no evidence of an interaction between burro type and season ($F_{2,16} = 1.71$, $P = 0.212$).

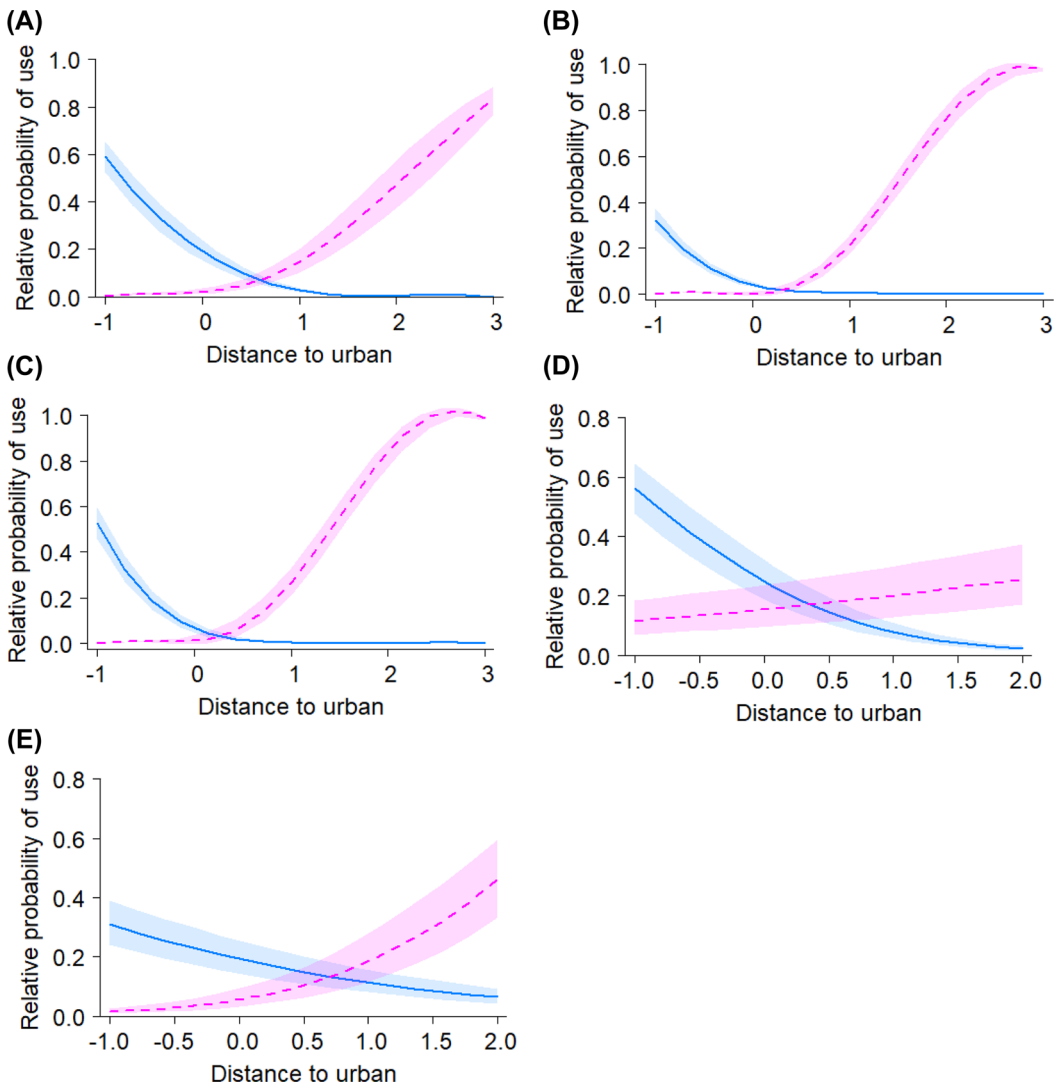


FIGURE 2 The predicted relative probability of use in relation to distance to urban areas (standardized) with 95% confidence intervals, between the close-range (blue line) and down-range burros (pink line) for global positioning system-collared burros at the Fort Irwin National Training Center, California, USA. Three seasons are presented at the landscape-scale: A) 2015 cool-wet season B) 2016 hot-dry season, and C) 2016 cool-wet season. Two seasons are presented at the home range scale: D) 2015 cool-wet season, and E) 2016 hot-dry season.

Frequency of water use did not differ between the 2 cool-wet seasons (mean difference = -9.95 ; 95% CI = -33.62 to 13.71 ; $P = 0.54$) or between the 2016 cool-wet season and the 2016 hot-dry season (mean difference = 16.99 hr; 95% CI = -6.68 to 40.67 ; $P = 0.19$). Water use did differ between the 2015 cool-wet season and the 2016 hot-dry season, however (mean difference = 26.95 hr; 95% CI = 3.27 – 50.62 ; $P = 0.024$).

Down-range burros spent an average of 4.7 ± 0.81 (SE), 3.9 ± 0.68 , and 2.2 ± 0.49 hours within 100 m of water sources during visits to water during the 2015 cool-wet, 2016 hot-dry, and 2016 cool-wet seasons respectively, whereas water visit duration of close-range burros was 2.7 ± 0.53 , 2.7 ± 0.44 , and 2.3 ± 0.33 hours during these same seasons. The median duration of water visits was shorter than the mean duration and was 1 hour in the 2015 cool-wet season and 2 hours in the 2016 hot-dry and cool-wet seasons for close-range burros and 4 hours, 2 hours,

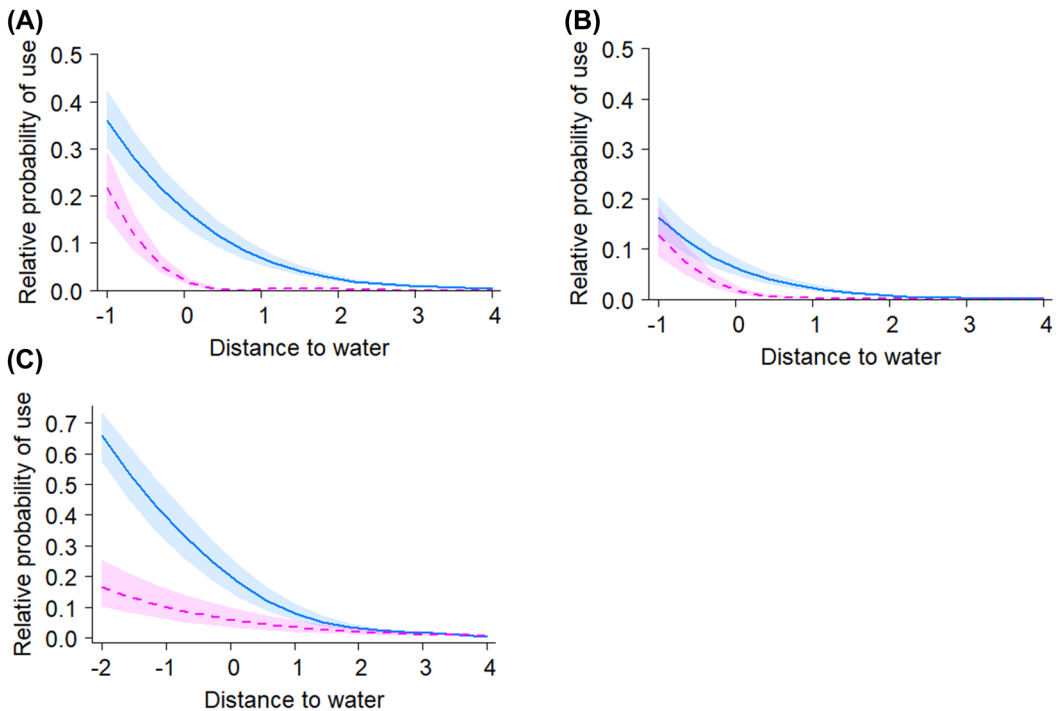


FIGURE 3 The predicted relative probability of use in relation to distance to water (standardized) with 95% confidence intervals, between the close-range (blue line) and down-range burros (pink line) for global positioning system-collared burros at the Fort Irwin National Training Center, California. Two seasons are presented at the landscape-scale: A) 2015 cool-wet season, and B) 2016 cool-wet season. One season is presented at the home range scale: C) 2016 hot-dry season.

and 1 hour during the 2015 cool-wet, 2016 hot-dry, and 2016 cool-wet seasons, respectively, for down-range burros. Mean duration of visits to perennial water sources by female burros did not differ by burro type ($F_{2,16} = 2.67$, $P = 0.141$), but duration of water visits differed by season ($F_{2,16} = 6.82$, $P = 0.007$) and there was a season by burro type interaction ($F_{2,16} = 3.67$, $P = 0.049$). Mean duration of water visits for close-range burros did not differ between seasons, but the duration of water visits for down-range burros was 2.5 hours longer (95% CI for mean difference = 0.79–4.3, $P = 0.010$) during the 2015 cool-wet season and 1.7 hours longer (95% CI for mean difference = 0.49–2.9, $P = 0.012$) during the 2016 hot-dry season compared to the 2016 cool-wet season.

DISCUSSION

Kernel home range estimates for GPS-collared females varied widely among individuals (23–430 km²), but contrary to our predictions there was no difference in home range size or core areas between seasons or burro types. The 95% MCP home range estimates for GPS-collared burros in our study were also variable among individuals (25–434 km²) with the average MCP size (166 ± 21 km² [SE]) being 3 to 12 times larger than home range estimates reported for burros in similar environments (Norment and Douglas 1977, Woodward 1979, Seegmiller and Ohmart 1981), although Norment and Douglas (1977) reported a few large home ranges up to 425.0 km². The mean home range size ranged from 19.5 km² to 68.0 km² in these other studies, and one reason for their smaller size might have been a result of different field methods. We employed GPS collars, whereas these other studies used

TABLE 3 Parameter estimates, lower and upper 95% confidence limits, z-scores, and *P*-values for variables in the highest-ranking seasonal models for home range scale habitat selection by global positioning system-collared female feral burros on the Fort Irwin National Training Center, California, USA, 2015–2017.

Variable ^a	β	SE	95% CI		z	P
			Lower	Upper		
Cool-wet season 2015						
(Intercept)	-1.37	0.18	-1.72	-1.02	-7.69	<0.001
Water	-0.55	0.01	-0.57	-0.53	-52.27	<0.001
NDVI	0.75	0.01	0.72	0.77	62.62	<0.001
Elevation	-0.48	0.02	-0.52	-0.45	-28.40	<0.001
Slope	-0.14	0.01	-0.17	-0.12	-11.41	<0.001
Urban	-1.36	0.03	-1.42	-1.29	-41.49	<0.001
Wash	0.004	0.01	-0.01	0.02	0.46	0.64
Δ NDVI	-0.07	0.01	-0.08	-0.06	-9.79	<0.001
Down-range	-0.58	0.33	-1.22	0.06	-1.79	0.07
Urban:down-range	1.68	0.06	1.57	1.79	29.67	<0.001
Slope:down-range	0.32	0.02	0.29	0.36	17.53	<0.001
Hot-dry season 2016						
(Intercept)	-1.01	0.18	-1.37	-0.65	-5.55	<0.001
Water	-1.04	0.01	-1.06	-1.01	-81.07	<0.001
NDVI	0.79	0.02	0.75	0.83	38.41	<0.001
Elevation	-0.90	0.02	-0.93	-0.87	-60.83	<0.001
Slope	-0.02	0.01	-0.03	0.00	-1.77	0.077
Urban	-0.63	0.04	-0.70	-0.55	-16.70	<0.001
Wash	-0.10	0.01	-0.11	-0.09	-13.94	<0.001
Δ NDVI	-0.13	0.01	-0.16	-0.11	-11.10	<0.001
Down-range	-1.42	0.34	-2.07	-0.76	-4.23	<0.001
Urban:down-range	1.96	0.06	1.84	2.09	31.42	<0.001
Water:down-range	0.46	0.02	0.42	0.49	24.42	<0.001
Cool-wet season 2016						
(Intercept)	-0.49	0.04	-0.57	-0.41	-12.04	<0.001
Water	-0.51	0.01	-0.53	-0.49	-51.79	<0.001
Elevation	-0.55	0.01	-0.58	-0.53	-41.92	<0.001
North	-0.12	0.01	-0.13	-0.10	-14.43	<0.001
Slope	-0.02	0.02	-0.07	0.02	-1.13	0.26
Wash	-0.03	0.01	-0.04	-0.01	-3.37	0.001
Mixed desert scrub	-0.11	0.03	-0.16	-0.06	-4.40	<0.001
Sparsely vegetated	-0.51	0.02	-0.55	-0.47	-24.55	<0.001

(Continues)

TABLE 3 (Continued)

Variable ^a	β	SE	95% CI		z	P
			Lower	Upper		
Minimum vegetated	-0.70	0.04	-0.77	-0.63	-19.25	<0.001
Playa	-1.83	0.08	-1.98	-1.68	-23.65	<0.001
Urban land cover	-0.45	0.05	-0.55	-0.35	-8.93	<0.001
Day	0.00	0.03	-0.05	0.05	0.04	0.97
Night	-0.05	0.02	-0.10	0.00	-2.12	0.03
Down-range	0.11	0.07	-0.03	0.25	1.54	0.12
Slope:day	0.01	0.03	-0.05	0.07	0.29	0.77
Slope:night	-0.22	0.03	-0.28	-0.17	-8.04	<0.001
Slope:down-range	0.03	0.03	-0.03	0.09	1.04	0.30
Day:down-range	-0.04	0.04	-0.12	0.04	-0.93	0.35
Night:down-range	0.07	0.04	-0.01	0.14	1.77	0.08
Slope:day:down-range	0.02	0.04	-0.07	0.10	0.40	0.69
Slope:night:down-range	0.14	0.04	0.06	0.22	3.54	<0.001

^aVariable notation: Urban = distance to urban area (m). Wash = distance to nearest wash (m). Water = distance to nearest water (m). NDVI = normalized difference vegetation index. Δ NDVI = change in NDVI. North = north aspect value. Down-range indicates the effect of burro type (close-range burros were the reference level). Day and night represent 2 of the 3 categories of diel period (crepuscular is the reference level). The land cover variable had 6 categories: playa, creosote bush-white bursage (reference), mid-elevation mixed desert scrub, sparsely vegetated, minimal vegetation, and urban land cover.

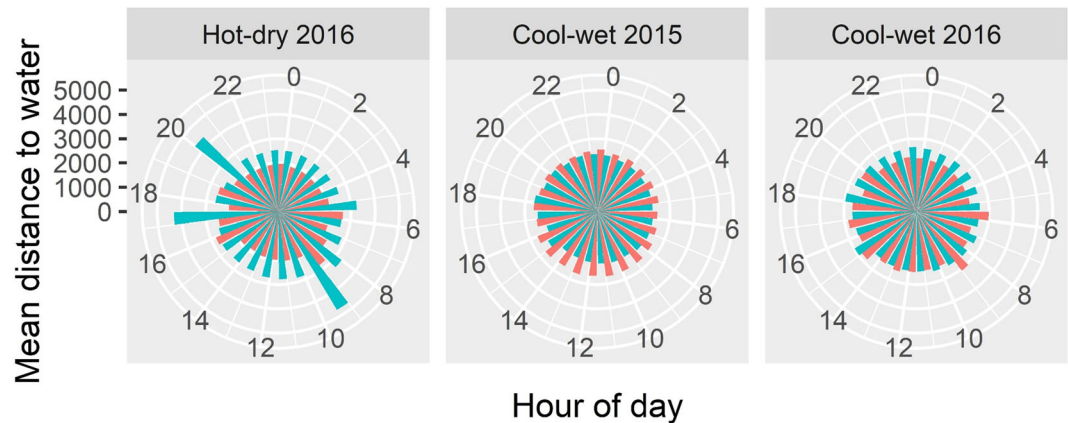


FIGURE 4 Mean distance between water sources and GPS locations collected on female feral burros at the Fort Irwin National Training Center, California, USA, during the hot-dry 2016, cool-wet 2015, and cool-wet 2016 seasons Close-range burros are in blue and down-range burros are in pink.

VHF collars resulting in comparatively few relocations (Norment and Douglas 1977, Woodward 1979, Seegmiller and Ohmart 1981). Asiatic wild asses (*Equus hemionus onager*) in the Negev Desert of Israel had relatively smaller home ranges with 50-day average home range size of GPS-collared asses being 23.6 km² and 31.3 km² for the summer and winter seasons, respectively (Giotto et al. 2015). In an arid area of India, the annual home range size of

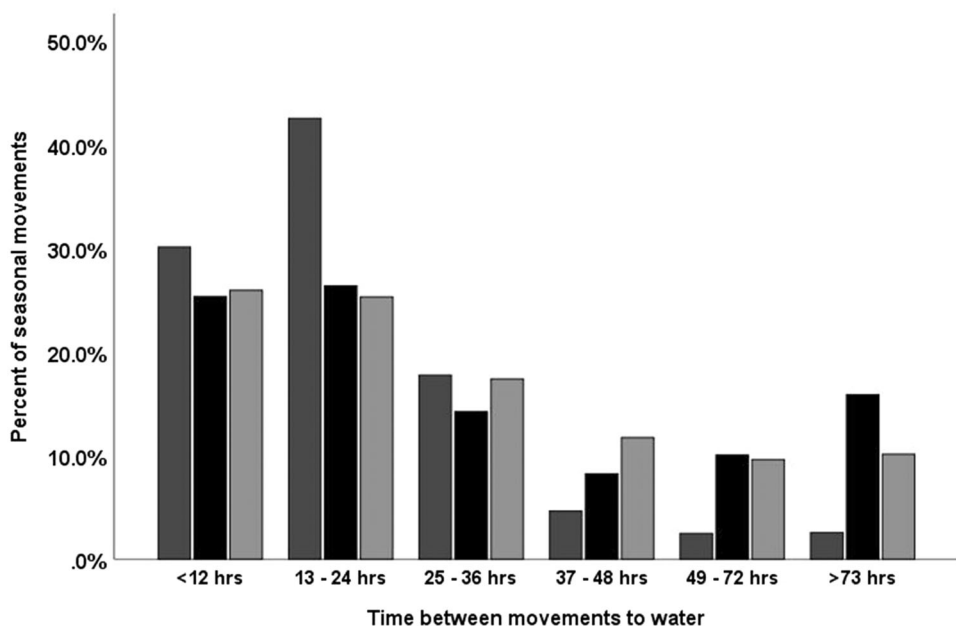


FIGURE 5 Visitation frequency to water sources by female feral burros at the Fort Irwin National Training Center, California during the hot-dry 2016 (dark gray), cool-wet 2015 (black), and cool-wet 2016 (light gray) seasons, November 2015 to March 2017.

female groups was 20.0 km² (Shah and Qureshi 2007). The GPS collars on burros in this study allowed for tracking 24 hours a day and may have provided a more accurate estimate of burro home range size or perhaps the distribution of resources in our system was sparse and widely spaced, necessitating larger home ranges to meet energy and water requirements. The lack of seasonal differences in home range size in our study could be related to the hierarchical nature of burro habitat selection with respect to essential resources. If the home range of individual burros was large enough to encompass resources sufficient to meet forage and water requirements or located on the landscape in such a way that their primary resource needs were met across the year, we would not expect to observe substantial seasonal changes in home range size. Burro home ranges were likely positioned on the landscape (second-order selection) based on the most limiting factor, which in this case was most likely distance to water. That said, our sample size and between-individual variation likely influenced our statistical power.

We expected that burro habitat selection would be primarily influenced by water dependency, forage characteristics, and thermoregulatory constraints, particularly during the hot-dry season. Resource selection by burros was most influenced by perennial water sources. Distance to water was a good predictor of burro resource selection followed by distance to urban environs, but the latter only applies to burros that had urban areas available to them. Urban areas included water sources and other resources, such as high-quality forage and thermal cover, and all of those resources were found in a relatively small area. Because these resources were spatially clumped, it is difficult to define which resources burros were focusing on inside the urban area. Burros also selected areas with high NDVI at all scales and seasons and consistently selected for lower elevation terrain; selection for other topographical features was variable.

Water influences the distribution and density of burros in desert climates and is a limiting resource for burros because of their reliance on water for thermoregulation and other physiological mechanisms (Cain et al. 2006, Grindler et al. 2006, Zakari et al. 2015, Esmaeili et al. 2021). Because burros are hindgut fermenters, they are generally less efficient in extracting nutrients (i.e., lower digestibility) and require more water for digestion (Janis 1976, Maloiy et al. 1979). Burros can compensate for their lower digestive efficiencies by increasing forage

consumption rates (Janis 1976); thus, the hindgut adaptation permits burros to thrive on a low-quality diet, frequently lower than that on which ruminants could maintain body condition (Duncan et al. 1990, Zakari et al. 2015). Their digestive inefficiency produces a large amount of wet feces (Maloiy et al. 1979, Cain et al. 2012) and their kidneys do not produce very concentrated urine (Schmidt-Nielsen 1964, Joubert and Louw 1976, Kihwele et al. 2020). Burros have a labile body temperature, which allows them to cope with increasing heat loads, but they also thermoregulate by evaporative cooling with sweat glands (Schmidt-Nielsen 1964). Consequently, equids frequently require more water than arid-adapted ruminants (Cain et al. 2006, 2012; Kihwele et al. 2020). Arid-adapted ruminants are generally less reliant on water than hindgut fermenters because the rumen can hold water up to 20% of the animal's body weight and acts as a buffer against dehydration and during rapid rehydration (Silanikove 1994, Cain et al. 2006). The movement of water from the rumen to the blood can help maintain blood plasma volume, preventing extreme dehydration and also protecting against the effect of osmotic shock due to rapid rehydration by slowly restoring osmotic homeostasis (Choshniak and Shkolnik 1977, Turner 1979, Silanikove 1994, Cain et al. 2006). Burros can drink large amounts of water (up to 30 L) at 1 visit without going into osmotic shock, which likely compensates for the increased water requirements for digestion and thermoregulation (Maloiy 1970).

Burros always selected for areas closer to water, but the strength of selection varied between spatial scales and seasons. With the exception of distance to urban areas, the magnitude of the parameter estimates for distance to water were generally twice as high as other continuous covariates at the landscape scale. Further, the magnitudes of the difference between the parameter estimates for distance to water and other continuous predictors were greater at the landscape scale compared to the within home range scale. The pronounced influence of perennial water sources on landscape-scale habitat selection of burros is likely related to the location of home ranges on the landscape relative to the spatial location of perennial water sources. The mean distance to permanent water from the home range centroids was $1,693 \pm 369$ m in the hot-dry season, $5,822 \pm 927$ m in the 2015 cool-wet season, and $3,028 \pm 558$ m in the 2016 cool-wet season. Burro home ranges were centered closer to perennial water sources during the hot-dry season and it appears that burro use of the landscape is such that water sources can easily be accessed from any part of their home range, particularly during the hot-dry season. This potentially reduces the influence of water sources on within home range habitat selection. Within their home ranges, female burros generally remained within 2.1–3.6 km of perennial water sources, being nearest to water during the hot-dry season as expected.

Burros on the NTC visited water sources at least once a day during the hot-dry season but typically visited water sources every 2 days during the cool-wet seasons. There were also long periods (>10 days) during the cool-wet season, and after it rained, when burros did not visit water sources and were likely getting water from forage or other ephemeral water sources that we were unable to map. During the hot summer months, burros in Arizona, USA, visited water daily, while during cooler months watering patterns were more sporadic and daily visits were reduced (Seegmiller and Ohmart 1981). Other ass species also change their movements around water sources on a seasonal basis. In the Gobi Desert, the mean distance from ass locations to water increased from 10.3 ± 2.9 km in summer to 15.8 ± 0.9 km in winter, and in the Negev Desert, asses visited water sources more often during the summer (1.33 ± 0.17 times/day) than in the winter (0.08 ± 0.05 times/day; Kaczensky et al. 2010, Giotto et al. 2015). During summer in Death Valley, California, male and non-lactating females drank approximately once every 24 hours (Moehlman 1998). Lactation is physically demanding for the female and greatly increases water requirements (Woodward 1979, Moehlman 1998, Cain et al. 2006). Females with young foals would drink 2 to 3 times a day and stay within 1.6 km of the water source (Moehlman 1998).

Recent work in nearby Death Valley National Park suggested that the timing of burro visitation to springs was related to mountain lion predation risk, with burro activity around water sources shifting towards a single peak in midday at springs where lion presence and kills were documented (Lundgren et al. 2022). Although mountain lions have been reported on Fort Irwin (Krzysik 1994), we did not document any during camera monitoring of springs on base (J. W. Cain, unpublished data). The timing of visits to water that we observed using collared females was

bimodal, with water visits generally occurring during late-morning through mid-day, with a second peak after sunset. Water use by female burros was neither evenly distributed across diel periods nor limited to midday when predation risk from mountain lions would be expected to be lowest. This bimodal pattern in water use was most pronounced during the hot-dry season, indicating that timing of water use was likely related to thermoregulatory constraints with burros foraging during the cooler hours of morning and evening, with trips to surface water largely relegated to midday and nighttime.

Urban areas can provide important resources for burros including water, forage, and thermal cover. Because urban areas provide multiple resources in a small area, we predicted that burros would select for areas closer to urban environs when available and that selection for urban areas would be stronger in the dry season. When urban areas were available, burros selected for these areas at both spatial scales and during all seasons with the exception of the 2016 cool-wet season at the within home range scale. Anecdotally, burros did not appear to be wary of humans, and used urban areas in all temporal periods and during all levels of human activity. When urban areas have higher quality resources than the surrounding areas and there are few negative consequences experienced when using urban areas, ungulates can habituate to human presence (Rubin et al. 2002, Lowry et al. 2013). In arid climates, urban areas can provide a consistent source of forage for ungulates that otherwise is not available during hot, dry periods (Rubin et al. 2002, Longshore et al. 2016). Similarly, bighorn sheep select for urban areas and forage on non-native plants found in urban areas more often in the summer when the nutritional quality of native forage species is lower (Rubin et al. 2002, Longshore et al. 2016). Ungulate use of urban areas can allow higher fitness for animals that are less reliant on rain or other natural processes to meet their resource needs. Urban landscaping uses irrigation to keep plants green and allows non-native plants to thrive in harsh weather conditions, providing animals in urban areas with food sources that are less affected by changes in precipitation compared to native forage species outside of urban areas (Longshore et al. 2016).

Forage conditions, as indexed by NDVI, also had a positive effect on burro habitat selection, appearing in 5 of the 6 top models. As expected, burros selected for areas with greener forage. Similar results have been reported for a variety of other herbivores (Marshall et al. 2004, Bro-Jørgensen et al. 2008, Acebes et al. 2012, Bartlam-Brooks et al. 2013, Creech et al. 2016). At the landscape scale and during the hot-dry season 2016, the close-range burros strongly selected for areas with higher NDVI, which were likely associated with urban areas. The influence of vegetation greenness on habitat selection of the down-range burros was minor because during the hot-dry season NDVI values were spatially similar; thus, there were few areas with higher NDVI that could be selected for. This was in contrast to the distribution of greenness available to close-range burros; during the hot-dry season, the urban area was much greener than the surrounding desert. Burros also selected for areas with lower rates of change in NDVI values, which means they selected for areas with more stable forage conditions, such as selecting for the creosote bush-white bursage vegetation type. Further, the vegetation types with the highest rates of change for NDVI were mid-elevation mixed desert scrub and playas. Mid-elevation mixed desert scrub tended to occur in rugged areas with steeper slopes, while vegetation contributing the NDVI change in playa areas was likely more ephemeral and related to periodic inundation following rains; playas had high rates of change but low overall NDVI. Even though ass species can digest low quality forage, previous studies report that, when available, asses selected areas with better forage conditions based on indices including NDVI, vegetation density, and forage greenness (Marshall et al. 2012, Hamrick et al. 2015, Malo et al. 2016). Precipitation during the 2015 cool-wet season was 60% below the long-term average, whereas during the 2016 cool-wet season, precipitation was 65% above average (Western Regional Climate Center 2016). Correspondingly, the magnitude of the parameter estimates for NDVI within each scale of the habitat selection analyses differed between the 2 cool-wet seasons with female burros showing a stronger positive response to NDVI and Δ NDVI during the drier 2015 cool-wet season. They also occurred closer to washes during the 2016 cool-wet season when higher rainfall would likely increase forage growth in washes.

While burros do have effective physiological mechanisms for thermoregulation, behavioral adaptations also play a major role in maintaining body temperature within physiologically acceptable limits (Cain et al. 2006, Xia et al. 2013, Zakari et al. 2015). Close-range and down-range burros selected for areas closer to washes, which in addition to providing

higher quality forage likely provided more thermal cover; ass species are known to use topography such as washes and different topographical aspects for protection from both heat and cold (Woodward and Ohmart 1976, Giotto et al. 2015). Aspect was only an important predictive variable in the 2016 cool-wet season when burros selected for southern aspects. While asses are reported to prioritize selecting cover over high forage indices during periods of thermal stress in summer, they also use southern aspects during cooler winter periods (Giotto et al. 2015); similar results were reported for desert bighorn sheep (Gedir et al. 2020). Burros also consistently selected for lower elevations, whereas the influence of slope on habitat selection was the least consistent, especially at the landscape scale. The high elevation regions of the study area were typically composed of steep slopes and rocky, rugged cliffs. These areas likely provided minimal vegetation and would be more difficult for burros to traverse (Acebes et al. 2012, Giotto et al. 2015). Burros typically use gentler slopes if forage is available in flatter terrain (Marshall et al. 2012, Malo et al. 2016).

The development of modern telemetry collars (e.g., GPS-Iridium) has facilitated advances in our knowledge of ungulate demography, movements, behavior, and habitat selection across a wide variety of species. Research on feral equids in the United States has lagged far behind that of other ungulates, including equids outside of the United States, resulting in extremely limited information for decision-making. Although there are some concerns with collar fit on equids, the lack of basic and applied ecological research on feral equids in the United States using modern telemetry collars is largely due to political considerations (Schoenecker et al. 2020, Boyce et al. 2021). To date, there have been few published studies using GPS collars on feral burros in the Southwest and the majority of previous research on feral burros used VHF telemetry resulting in limited relocation and movement data. Fitting feral burros with GPS collars would provide more informative data on burro demography, movements, and habitat use. Although we were only able to collar a limited number of adult female burros, we believe that our results would be applicable to female burros in other populations occupying predominantly wildland areas (i.e., our down-range burros) with similar vegetative and climatic conditions, and those occupying areas near urban areas (e.g., Kingman, AZ; BLM 2022c). We did not fit males with GPS collars, so our results only apply to females. In addition, given the variation in habitat conditions in areas occupied by feral burros in the Southwest, further research on sex-specific habitat selection and movements on other populations would benefit decision-making.

Overall, distance to water and distance to urban areas were the most important habitat characteristics influencing habitat selection of female burros on Fort Irwin. The need for female burros to water every 1–2 days and the limited distribution of perennial water sources on Fort Irwin strongly influences female burro habitat selection at the broadest spatial scales.

MANAGEMENT IMPLICATIONS

Managers could exploit the reliance of feral burros on a few perennial water sources for fertility control efforts by darting females with immunocontraceptives (or other birth control agents) at these locations. Because the most common immunocontraceptive requires repeated doses to remain effective, having individually identifiable (e.g., branded, collared, or both) burros would be necessary. Much of the human–wildlife conflict on the NTC is caused by the close-range burros. Limiting burro access to sources of surface water and other resources in urban areas could aid in reducing burro use of these areas where the greatest human–wildlife conflict occurs. Our results suggest that limiting burro access to natural and anthropogenic water sources could reduce their use of such areas. Water availability in urban areas can be limited by blocking off access to irrigation ditches and sewage treatment ponds, and converting urban landscapes to more xeric vegetation, by including native plant species that require less water. These actions may reduce the attractiveness of urban areas to burros. Although burros could access ephemeral water sources such as playas during the rainy season, permanent water sources in arid areas are often relatively small and contained and access to these sources could be restricted. Down range, fencing that allows access by native wildlife, such as bighorn sheep, but precludes burro use could be used.

ACKNOWLEDGMENTS

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government. We thank A. Neibergs, G. Lockie, and the staff of the BLM Ridgecrest Wild Horse and Burro Facility for advice and assistance with corral trapping. We thank L.M. Aker, C. A. Everly, D. Housman, I. D. Rahkmanov, J. L. Nierman, and O. J. Alcumbac for their assistance. We thank K. A. Schoenecker and 2 anonymous reviewers for their insightful reviews of an earlier version of this manuscript. We thank New Mexico State University Agricultural Experiment Station, NTC Fort Irwin Directorate of Public Works, and the United States Army Corps of Engineers: Construction Engineering Research Laboratory for funding.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All procedures were approved by the New Mexico State University Institutional Animal Care and Use Committee (permit 2015-002).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Associate Editor: Kathryn Schoenecker.

SUPPORTING INFORMATION

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How to cite this article: Karish, T., G. W. Roemer, D. K. Delaney, C. D. Reddell, and J. W. Cain, III. 2023. Habitat selection and water dependency of feral burros in the Mojave Desert, California, USA. *Journal of Wildlife Management* 87:e22429. <https://doi.org/10.1002/jwmg.22429>