Journal of Arid Environments 200 (2022) 104728

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Limited resources shape home range patterns of an insular ungulate in a semi-arid ecosystem

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ARTICLE INFO

Keywords:
Home range selection function
Home range size
Mule deer (Odocoileus hemionus fulinginatus)
Ungulate

ABSTRACT

Understanding patterns of home range size and selection are critical to protect vulnerable wild populations, particularly in semi-arid regions with increasing land use pressures. Using movement data from 64 GPS-collared southern mule deer (*Odocoileus hemionus fulinginatus*), monitored over two years in San Diego County, we assessed patterns and drivers of home range following a two-step approach. First, we implemented seasonal home range selection functions to examine variation in selection and avoidance of environmental factors. We then used these results to evaluate the relative impact of environmental factors in combination with intrinsic factors on home range size. We found that deer use of high-quality forage and water sources varied seasonally. These variations in resource use, along with sex and age, played a role in determining home range size of the southern mule deer. Home range size was larger for male deer, and smaller among older females. Home ranges for both sexes were smaller when forage quality increased and larger with greater variability in water proximity. The limited resources of semi-arid environments, like water and forage, affect southern mule deer populations and highlight the importance of evaluating combined intrinsic and extrinsic factors of home range size and composition to inform management practices.

1. Introduction

Space use and home range are fundamental concepts in ecology (Burt 1943) used to describe an organism's relationship with its environment. They are integral to the study and understanding of key ecological patterns and processes such as habitat selection (Harris et al., 1990), community structure (Gompper 2002), distribution of organisms and populations (Wang and Grimm 2007), competition and territoriality (McNab 1963), and predator-prey dynamics (Lewis and Murray 1993). While considerable research has focused on delineating and quantifying home ranges, the extrinsic environmental factors that influence home range selection and the interaction of intrinsic and extrinsic factors that influence home range size are less understood (Powell and Mitchell 2012), particularly in arid and semi-arid environments where resource limitations may affect home range composition, distribution, and size.

With advances in GPS and radio-tracking technology, a large body of research has found that age, sex, body size, and reproductive status influence home range characteristics, such as size and habitat quality (McNab 1963; Harestad and Bunnel 1979; Lindstedt et al., 1986; Swihart et al., 1988; Cederlund and Sand 1994). Extrinsic landscape factors have also been found to have significant influence on an individual's home range, including human disturbances (Riley et al., 2003), topography (Walton et al., 2017), as well as seasonal changes in water availability and vegetation composition (Taber and Dasmann 1958; McKee et al., 2015; Pérez-Solano et al., 2017). Both the extrinsic and intrinsic drivers of home range composition and size have been associated with home range shifts throughout the year as a function of changes in resource availability and metabolic constraints of the animal (Tufto et al., 1996).

Intrinsic influences on home range size and composition can vary over time, depending on the resource needs of the animal (Tufto et al., 1996). In several animal taxa, males tend to have larger home ranges than females to retain more breeding opportunities, a pattern that remains fixed through time (Aronsson et al., 2016). On the other hand, intrinsic characteristics that reflect biological changes over time, including reproductive status (e.g., rutting or fawning in deer), age, and body size, can also play a role in the animal's resource needs and

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https://doi.org/10.1016/j.jaridenv.2022.104728
Received 5 July 2021; Received in revised form 20 January 2022; Accepted 23 January 2022
Available online 9 February 2022
0140-1963/

requirements, which in turn influence home range composition and size. For example, animals caring for offspring often have significantly larger home ranges to support their increased resource needs (Cederlund and Sand 1994; Tufto et al., 1996), signaling the relationship between space use and changes in an animal's intrinsic characteristics.

Habitat quality, i.e., resources, and other extrinsic environmental factors vary both spatially and temporally and can be reflected in an animal's habitat use and selection (Fryxell et al., 2008; Hooten et al., 2014). For many herbivores, home range composition has been linked to vegetation productivity (Byrne et al., 2014), which can vary depending on the year, season, or even time of day (Fryxell et al., 2008; Hooten et al., 2014). As a result, many animals shift spatial distribution seasonally in response to vegetation productivity and precipitation (Boone et al., 2006; Tsalyuk et al., 2019). For example, resident black-tailed deer exhibit seasonal shifts in home range in response to changes in vegetation and microclimates on north-to south-facing slopes (Taber and Dasmann 1958), demonstrating the importance of habitat quality to herbivore populations.

Water is another critical resource that influences habitat quality and variations in water availability between dry and wet seasons can create significant shifts in home range location and size in response to available water sources (McKee et al., 2015; Pérez-Solano et al., 2017). In the arid and semi-arid ecosystems of California, droughts are recurring events and climate models predict greater intensity and frequency of droughts in the future (Diffenbaugh et al., 2015; Mann and Gleick 2015), further limiting water resources. California's most recent drought was the hottest and driest on record, spanning a period of seven years, and ending after an unusually wet winter in the 2018–2019 water year. While the threat of limited water for human use is well understood in California and other arid regions that suffer from drought and increasing aridity, the underlying consequences for wildlife and their habitats is often overlooked.

Intra-annual or seasonal changes in home range size and composition are most prominent in migratory or transitory animals (Albon and Langvatn 1992), however insular, non-migratory animals also exhibit home range shifts throughout the year as a function of changes in local resource availability and an organism's metabolic constraints (Tufto et al., 1996). In this study, we investigated the influence of intrinsic and extrinsic factors on home range size and habitat selection of the southern mule deer (*Odocoileus hemionus fulinginatus*) a non-migratory, harvested ungulate that is native to the semi-arid habitats of southern California and the Baja peninsula whose populations have been reported to be declining (Bohonak 2012). We used telemetry and landscape data to explore how southern mule deer habitat selection differs seasonally and consider how changes in extrinsic environmental factors along with intrinsic demographic factors influence home range size. For insular ungulates, changes in landscape use relative to extrinsic environmental and intrinsic demographic factors may occur on smaller scales but provide key information needed to support management and conservation practices. In particular, in semi-arid landscapes like southern California where land pressure is intensifying with increased urbanization, fires, and droughts, understanding the patterns and trends of home range size and selection will be critical to preserve and protect vulnerable wildlife.

2. Methods

2.1. Study area and deer capture

This study was conducted in San Diego County, CA, USA. San Diego has a Mediterranean climate consisting of cool, wet winters (average precipitation during study period = 58.0 mm) and hot, dry summers (average precipitation during study period = 2.3 mm), where rain typically starts at the end of October and ends by the month of April. Southern mule deer were captured within three study areas representing the range of habitat types available to deer in San Diego County comprising of public and private lands; San Felipe Valley, Kitchen Creek, and Rancho Jamul (Fig. 1). San Felipe Valley is a state wildlife area on the western border of Anza-Borrego Desert State Park, which we segmented into two sub-areas: San Felipe Valley and San Felipe Hills, separated by a county highway, S-2 (Fig. 1, Fig. S1). This area receives an average of 61 mm of precipitation in the wet season in the form of either snow or rain, and has an elevation of 700–1500 m. Several private rural ranches and homes and two highways intersect the study area. The area consists of transitional vegetation types including oak woodland, interior sage scrub, chaparral, desert riparian woodland and Sonoran Desert scrub. Kitchen Creek is in the southwest corner of the Cleveland National Forest in the Kitchen Creek watershed. It is adjacent to a major interstate, I-8, has an elevation of 900–1800 m, and receives an average annual precipitation of 65 mm. Vegetation within the study area largely consists of chaparral and Great Basin sagebrush. Kitchen Creek is adjacent to several large ranches and two tribal reservations as well as several recreational and administrative facilities on National Forest lands. The Rancho Jamul study site includes Rancho Jamul Ecological Reserve and Hollenbeck Canyon Wildlife Area. These two areas are separated by a state highway, State Route 94, and are surrounded by private residential and agricultural land. The Wildlife Area consists largely of riparian and sage scrub habitats and has many rural residential housing units around its border. The Ecological Reserve is used for cattle grazing and is adjacent to a large casino, multiple trailer parks, and is often used for U.S. Customs and Border Patrol operations. The area receives an average of 52 mm rainfall and has an elevation of 200–1100 m. The vegetation of Rancho Jamul is characterized as disturbed grassland, coastal sage scrub, and willow-sycamore riparian woodlands. The San Felipe Valley and Kitchen Creek study areas allow seasonal tag hunting of southern mule deer.

We conducted field work from February 2018 to January 2020 in the early fall and spring. All animal capture and handling was performed in accordance with state protocols and in compliance with the laws, policies, and guidance required by the institutional animal care and use committee (IACUC approval ID APF # 17-09-009L). In total, we captured 100 Southern mule deer (17 males, 83 females). We netted deer from helicopters and processed and collared them without sedation in the field. During capture we measured each deer, assessed age based on tooth eruption and wear (Erickson et al., 1970), and fit animals with LiteTrack360 Iridium GPS collars (Lotek Wireless, Inc., Ontario, Canada). We programmed all collars to record GPS locations at a 7-hr interval to allow each hour of the day to be recorded on a weekly basis, limiting bias towards certain time periods of the day. Every location record included UTM coordinates, altitude, dilution of precision, fix status, and temperature. The average time of collar deployment was 540 days and ranged 9–841 days. Shorter periods of deployment occurred due to deer mortality ($n = 36$), collar malfunctions ($n = 10$), or collar loss. Deer mortality was largely attributed to predation ($n = 16$) and vehicular collisions ($n = 6$), with few incidents of capture myopathy ($n = 3$). Since the start of the study, a total of 81 collars were deployed. When available, we retrieved collars from deceased deer to refurbish and re-deploy ($n = 23$) them in subsequent capture periods, allowing for 100 total deer captures. We removed all unreliable GPS locations (dilution of precision >5, fix status ≤ 2-D) before analysis.

2.2. Data analysis

To evaluate changes in landscape and habitat use and the influences of intrinsic and extrinsic factors on southern mule deer home range size, we followed a two-step approach using calculated seasonal deer home ranges. First, to identify extrinsic factors that may be important to southern mule deer, we implemented a home range selection function (HRSFs or second order selection; Johnson 1980) using a binomial generalized linear mixed model, where the extent for sampled environmental data was derived from each seasonal deer home range. Then, we assessed the relative importance of intrinsic factors in combination

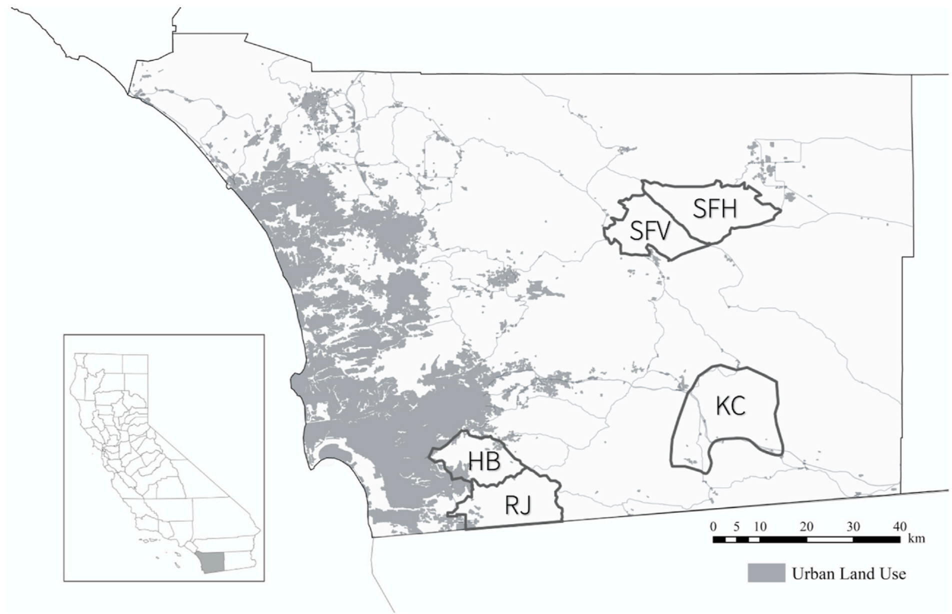

Fig. 1. Southern mule deer study area located in San Diego County, CA, USA. The study sites include San Felipe Valley (SFV), San Felipe Hills (SFH), Kitchen Creek (KC), Rancho Jamul Ecological Reserve (RJ), and Hollenbeck Canyon Wildlife Area (HB). Urban land use and roads are depicted to illustrate variation in anthropogenic land use pressure among sites.

with the extrinsic factors we found to be significant in our HRSF. For this second analysis, we assessed 12 candidate mixed effect linear regression models representing different hypotheses regarding the importance of intrinsic and extrinsic variable classes.

Our study encompassed a period of two years, where we utilized GPS data from collared individuals from May 2018 through March 2020. We calculated home ranges for southern mule deer in both the wet season, defined as November 1 through April 30, and the dry season, defined as May 1 through October 31, to capture seasonal variation. We calculated separate seasonal home ranges for each individual that had at least 15 GPS points for each month of the season ($n > 90$). From this, we calculated a total of 184 distinct 6-month long seasonal (94 wet and 90 dry) home ranges from 99,264 ($\mu = 539.5$, range = 90–650) locations recorded for a total 64 deer. All Analysis were conducted using R 3.5.0 (R Development Core Team, 2019) and ArcGIS 10.6 (ESRT, Redlands, CA software), unless otherwise stated. All regression analysis were implemented with the 'lme4' package (Bates et al., 2019).

We estimated home ranges for use in both HRSF and home range size analysis using the Local Convex Hull (LoCoH) method (Getz and Wilmers 2004; Getz et al., 2007). A multitude of methods are used to calculate animal home ranges, but in study areas where hard boundaries like roads are prevalent, animal space use can be more accurately represented with LoCoH estimation, which is designed to reflect the hard edges of barriers to movement (Getz et al., 2007). We calculated home ranges using the adaptive sphere of influence (a-LoCoH) method, which is the recommended variation of LoCoH by Getz et al. (2007) as it is less sensitive to the specification of the kernel parameter. Due to the robustness and flexibility of this parameter at the upper limits, we set a standard value of a = 10 km. We adjusted a-values as needed to ensure 100% isopleths with no holes or gaps. We estimated 50 and 90% isopleths in square kilometers for each seasonal home range. We defined the 90% isopleth as the animal's home range to be used in regression analysis, following Börger et al. (2006) and Getz et al. (2007). LoCoH home ranges were calculated in the R package 'adehabitatHR' (Calenge 2020).

We explored seasonal movement shifts of deer home range between the wet and dry season by comparing distance between home range centroids and home range percent overlap. We calculated home range centroids using the centermost point of each 50% isopleth home range. Then for each individual deer, we measured the distance between all consecutive seasonal centroids as well as the distance between the same seasons, where available. We statistically compared centroid distances between the same (dry-dry & wet-wet) season, and different seasons (dry-wet) using a standard *t*-test. We similarly measured the percent overlap of all consecutive seasonal home ranges (e.g., Dry, 2019-Wet, 2019) and same season home ranges (e.g., Dry, 2018-Dry, 2019) for each individual deer. We then compared the percent overlap between the same and different seasonal home ranges using a standard *t*-test.

2.3. *Environmental data*

We evaluated environmental variables (n = 19) that could influence mule deer habitat use: topography, land cover type, spectral vegetation index, human development, and climate (Table S1). All variables had a 30m spatial resolution except for the climate variables (climatic water deficit, precipitation, maximum temperature, and minimum temperature) which had a resolution of 90m. Climatic variables were available on a monthly basis, so we calculated averages for each season (Dry, 2018; Wet, 2019; Dry, 2019; Wet, 2020) and attributed values to the appropriate home range. We calculated the normalized difference vegetation index (NDVI) from bands 4 and 5 of Landsat 8 satellite imagery (USGS and EROS, Landsat 8 OLI/TIRS Collection 1 reflectance data) using ArcGIS NDVI image analysis. We converted all images with minimal cloud cover over each study area into NDVI, averaged by pixel over each season, and then assigned to the appropriate home range. This resulted in a total of seven NDVI maps used for each season except for the Wet 2019 season where only two images had a suitable cloud cover. To assess the importance of water availability, we evaluated Euclidean distances to ephemeral, permanent, and artificial water sources. The combination of distance to artificial or permanent water sources performed the best in initial models and was chosen for use in further analyses. We assessed the influence of roads by testing different road classifications (tertiary, secondary, etc.) across a range of scales by applying Gaussian smoothing to each surface using the 'smoothie' R package (Gilleland 2015). We tested both water and road classification surfaces at scales ranging from 90 m to 2160 m to assess the variation in scale that southern mule deer respond to most strongly and selected the best performing representation for our models. The largest scale was based on previous knowledge of deer dispersal distances. The most robust scale for both roads and water was 180 m, which we applied to the remainder of our analysis. We normalized each independent continuous variable prior to analysis by scaling using the method of subtracting by the mean and dividing by the standard deviation (Gelman 2008). Land cover types were used categorically in our models.

2.4. Home range selection function

To elucidate extrinsic environmental variables associated with southern mule deer home ranges, we employed a HRSF for each season over the two-year study period. HRSFs were developed using a binomial 'used' versus 'available' framework (Johnson 1980; Johnson et al., 2006). To build our models we first considered points randomly distributed in an individual's LoCoH home range as used and points randomly distributed in a buffer around that home range as available. To create an available area, we took the maximum distance between points used in the creation of each home range, averaged this value for all home ranges (average = 6120m), and buffered each individual home range by this distance. We calculated the mean number of points to create each seasonal LoCoH home range, 450 (range = 90–853), and randomly distributed this number of points within each used and available area, creating a 1:1 ratio of used to available points.

To evaluate preferred and avoided habitat variables for the HRSF in southern mule deer for each season we built generalized linear mixed-effect models with a binomial distribution (1 = used, 0 = available) using the logit link function, with individual as a random effect. We first tested each variable (Table S1) for univariate significance. We compared variables that we found to be significant for each season in a Pearson's correlation test, and then considered all possible model combinations without correlated variables ($r > |0.60|$). Final models for each season were evaluated using Akaike's Information Criterion (AIC) (Akaike 1973) and Bayesian Information Criterion (BIC) (Schwarz 1978).

To further explore deer use of specific vegetation types and the relationship between vegetation quality (NDVI) and vegetation type, we plotted the spatial extent (proportion of total area) and NDVI for six detailed vegetation cover types as well as the broad land cover types that have been identified as important to southern mule deer in a nearby transmontane habitat (Colby 2008). For each of these cover types – acacia scrub, Diegan coastal sage scrub, montane buckwheat scrub, chamise chaparral, semi-desert chaparral, and mesquite bosque – we calculated proportion of total area per type within deer home ranges and the total study area.

2.5. Home range size analysis

First, we evaluated whether LoCoH home range sizes differed significantly by year, season, sex, or study area with bar plots and Kruskal-Wallis tests (Kruskal and Wallis 1952) as the data did not meet assumptions for an ANOVA, including non-normal distributions and heterogeneity of variance. We found that home range size did not significantly differ either between seasons or years, so we opted to run one full model with all 184 seasonal home ranges to increase the power of our models, as opposed to running separate analysis for each season or year. We log-transformed home range size to improve the normality of distribution (skew = 0.11), as the previous distribution was positively skewed (skew = 1.47). To evaluate the importance of extrinsic factors in home range size, we used the environmental variables identified in our final selected HRSF model. We calculated the average and standard deviation of each raster surface from the seasonal HRSFs for each home range. To reduce the number of variables in our candidate models we then ran univariate linear regression models for both the mean and variance of each variable, compared them for significance using Akaike's Information Criterion for small sample size correction (AICc) (Burnham and Anderson, 1998), BIC (Schwarz 1978), as well as in correlation tests to determine the most appropriate variables to include in our mixed-effect (GLMM with logit link function) candidate models. We found a strong correlation between variation in climatic water deficit (CWD) and variation in precipitation ($r = 0.66$), where CWD performed better in models, so we removed precipitation from our home range size analysis. We also included the intrinsic variables of sex, age, and size (measured as girth in mm) in our analysis. In preliminary testing of these factors, the size of the animal was not a significant predictor of home range size, so we did not include size as a factor in our models.

In our home range size analysis, both geographic area and individual had the potential to significantly influence the intraspecific variance seen among home range size models. Specifically, it is intuitive to expect that seasonal home range sizes from a single individual is likely be more similar to each other than home ranges from another individual. Similarly, individuals captured in the same study area would be more likely to have comparable home range sizes to one another relative to individuals in a different study area due to site-specific conditions that may not be captured in the regression models. Because the intraspecific-variance structure of home range size can be influenced by these different random factors, we used a hierarchical mixed effects approach employed in previous home range size studies (Börger et al., 2006; Zuur et al., 2009) to determine the best random effect structure for our mixed-effect regression models. To do this, we tested for the best random component to use in our regression models by fitting a mixed effect model with all explanatory variables described above as constant fixed effects, and then varied the model by testing different levels of each random effect. With our fixed effects constant, we evaluated four possible random effect models: (1) no random intercept (ordinary least squares model), (2) individual as random effect, (3) study area as random effect, and (4) individual nested in study area as random effect. We evaluated the models using AICc and likelihood ratio tests to determine the best model structure (Zuur et al., 2009) and determined that a random intercept model with individual as the random effect was best for our regression analysis.

Due to either deer mortality, collar failure, or timing of capture, 8 out of 64 (12.5%) individuals in our study had only one seasonal home range and 56 individuals had 2-4 seasonal home ranges. To confirm that these singular measures did not have undue influence in our random intercept models, we ran a subset of our models with these individuals removed to confirm that the coefficients and trends remained constant.

To explore the relationship between our selected fixed effects and home range size, we developed 12 candidate models (Table 1) that represented varying classes of factors we deemed important to southern mule deer. We based these hypotheses from the HRSFs in our previous steps. We calculated Akaike weights based on AICc for each model to determine the best candidate model. To quantify the importance of

Table 1
Candidate models for understanding the variation in home range size of southern mule deer. As the demographic variables of sex and age could possibly affect or influence one another, we calculated these fixed effects as an interaction, but assumed no interactions were present among extrinsic variables.

Model Name	Variables
Intercept Only	–
Intrinsic	(Age:Sex)+Sex
Topographic	Elevation(μ)+Slope(μ)
Preferred	Slope(μ)+CWD(σ)
Avoided	Elevation(μ)+AllRoads(σ)
Varied	NDVI(μ)+Water(σ)
Extrinsic Global	Elevation(μ)+Slope(μ)+AllRoads(σ)+CWD(σ)+NDVI(μ)+Water(σ)
Intrinsic + Topo	(Age:Sex)+Sex + Elevation(μ)+Slope(μ)
Intrinsic + Prefer	(Age:Sex)+Sex + Slope(μ)+CWD(σ)
Intrinsic + Avoid	(Age:Sex)+Sex + Elevation(μ)+AllRoads(σ)
Intrinsic + Varied	(Age:Sex)+Sex + NDVI(μ)+Water(σ)
Intrinsic + Extrinsic Global	(Age:Sex)+Sex + Elevation(μ)+Slope(μ)+AllRoads(σ)+CWD(σ)+NDVI(μ)+WaterDist(σ)

individual variables in our best model we used the method of hierarchical partitioning in the R package 'hier.part' (Walsh and Mac Nally 2020). This method calculates the independent effect of each variable to the explanation of variance in the response variables across all variable combinations to provide a visualization and evaluation of the relative importance of the predictor variables in our best candidate model.

3. Results

From the 184 southern mule deer 6-month seasonal LoCoH home ranges we calculated; size varied from 0.42 km^2 (female deer in San Felipe Valley in the Dry, 2019 season) to 4.50 km^2 (male deer in San Felipe Hills in the Wet, 2019 season). The average southern mule deer home range size was 1.45 km^2 (female = 1.32 km^2, male = 2.68 km^2). We found the average home range size for the wet seasons was 1.50 km^2 (female = 1.35 km^2, male = 2.97 km^2) and the average home range size for the dry seasons was 1.40 km^2 (female = 1.29 km^2, male = 2.39 km^2).

We found no significant difference in home range sizes between seasons and years ($p = 0.38$), although we did observe a significant difference in sizes between sexes ($p < 0.01$) and among the study areas ($p < 0.01$). Home range sizes for female deer in the Rancho Jamul study area were significantly smaller than home ranges in the Kitchen Creek and San Felipe Hills study areas (Table 2).

We found that the home range centroid distance for individual deer between the same (dry-dry, wet-wet) and different (dry-wet) seasons was also not significant. However, the percentage of home range overlap between the same and different seasons was significantly different ($p = 5.47e^{-07}$), with percent overlap for the same season being significantly higher than percent overlap between seasons.

3.1. Home range selection function

Habitat selection varied significantly from the wet to dry season, although we found that some landscape features were important to home range selection across seasons. In both seasons, deer selected areas with steeper slopes, lower elevations, and higher climatic water deficit (CWD), while avoiding areas with greater road densities (Table 3, Fig. 2). In the wet season, deer selected areas with higher NDVI values and precipitation while in the dry season they selected areas closer to available water (Table 3, Fig. 2). Vegetation and land-cover types were not significant factors for home range selection in either season. However, when we evaluated the prevalence of specific vegetation types within deer home ranges we found that deer disproportionately used some vegetation types (e.g., acacia scrub, Diegan coastal sage scrub, chamise chaparral, semi-desert chaparral, montane buckwheat scrub, and mesquite bosque) relative to their availability across the study area (Fig. S2). Seasonally, NDVI values per vegetation type tended to be higher in the dry season, except for coastal sage scrub (Fig. S3).

3.2. Intrinsic and extrinsic drivers of home range size

We found that individual was the best performing random effect in our home range size analysis (AICc = −166.78), as opposed to study area (AICc = −139.45), individual nested in study area (AICc = −165.09), or no random effect (AICc = −138.59). Using the likelihood ratio test (LR = 33.46 and $p < 0.01$), we established it was necessary to include individual as a random effect in our models. We found that individuals with only a single home range did not influence the trends of our analyses.

Based on our analytical approach, we found two competing models best explained the factors associated with home range size. From these two models, we selected the top model of Intrinsic + Varied, as this model was inclusive of all the variables in the second supported model, Intrinsic only. Our top model included both intrinsic variables as well as extrinsic factors that varied between wet and dry seasons. The two most influential extrinsic factors were NDVI and distance to water (Table 4), whereas age and sex were the intrinsic factors associated with significant differences in home range size among southern mule deer. Our

Table 2
Average home range size of southern mule deer between study areas located in San Diego County, CA, USA, where n is the number of home ranges calculated by area across seasons and year.

Study Area	Average HR Size	Female HR size	Male HR size
San Felipe Hills	1.81 km^2 (n = 49)	1.72 km^2 (n = 47)	3.87 km^2 (n = 2)
San Felipe Valley	1.46 km^2 (n = 45)	1.30 km^2 (n = 37)	2.21 km^2 (n = 8)
Kitchen Creek	1.79 km^2 (n = 15)	1.62 km^2 (n = 13)	2.89 km^2 (n = 2)
Rancho Jamul	1.02 km^2 (n = 53)	0.94 km^2 (n = 51)	3.17 km^2 (n = 2)
Hollenbeck Canyon	1.45 km^2 (n = 22)	1.18 km^2 (n = 18)	2.68 km^2 (n = 4)

Table 3
Beta estimates and 95% confidence intervals for predictors of mule deer home range selection in wet and dry seasons based on GLMM HRSF modeling. Estimated values represent change in the log-odds of home range occurrence per unit change in the standard deviation of each covariate. Precipitation was a significant variable used in the wet season model, but not in the dry season model.

Variable	Wet Season			Dry Season		
Fixed Effect	Estimate	Lower Limit	Upper Limit	Estimate	Lower Limit	Upper Limit
Intercept	−0.03	−0.36	0.30	0.04	−0.31	0.38
Percent Slope	0.17	0.15	0.18	0.02	7.62E-3	0.04
Elevation (m)	−1.40	−1.44	−1.36	−1.45	−1.50	−1.40
Primary Roads	−0.48	−0.52	−0.44	−0.51	−0.54	−0.48
Secondary Roads	−0.08	−0.11	−0.06	−2.90E-4	−0.02	0.02
Tertiary Roads	−0.61	−0.63	−0.58	−0.70	−0.73	−0.67
NDVI	0.22	0.20	0.24	−0.02	−0.04	3.05E-4
Water Proximity	−0.08	−0.09	−0.06	0.09	0.08	0.11
Climatic Water Deficit	0.41	0.38	0.44	0.13	0.11	0.15
Precipitation	0.34	0.31	0.36	–	–	–

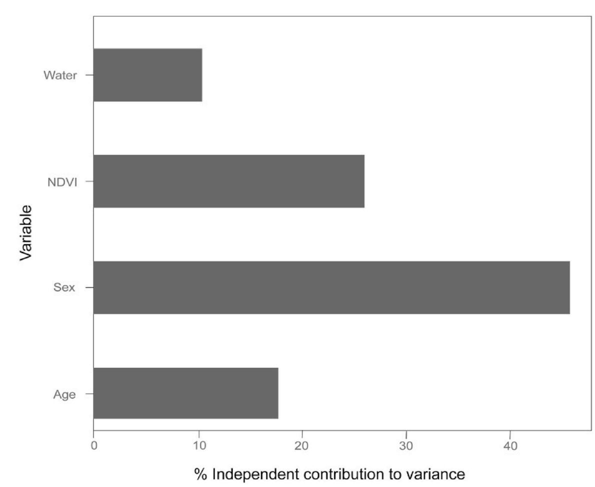

Fig. 2. Percent influence of each variable from our final candidate models on southern mule deer home range size based on a hierarchical partitioning model. Extrinsically, NDVI had a negative relationship to home range size while proximity to water was positively related. Intrinsically, male deer had larger home ranges, while older female deer had smaller home range sizes (Table S2 for detail).

Table 4
Results of mixed effect candidate models of southern mule deer home range size.

Model	AICc	Delta AICc	Relative Likelihood	AICcWt	Restricted LogLik	Cum.Wt
Intrinsic + Varied	−124.62	0.00	1.00	0.58	70.72	0.58
Intrinsic	−123.93	0.68	0.71	0.41	68.20	0.99
Intrinsic + Topo	−114.86	9.76	0.01	0.00	65.84	0.99
Intrinsic + Avoid	−114.28	10.31	0.01	0.00	65.55	1.00
Varied	−105.46	19.16	0.00	0.00	57.90	1.00
Intrinsic + Prefer	−102.83	21.79	0.00	0.00	59.82	1.00
Intercept Only	−99.78	24.84	0.00	0.00	52.95	1.00
Intrinsic + Extrinsic Global	−98.72	25.89	0.00	0.00	62.28	1.00
Topographic	−97.66	26.96	0.00	0.00	54.00	1.00
Avoid	−93.87	30.75	0.00	0.00	52.10	1.00
Extrinsic Global	−83.94	40.68	0.00	0.00	51.48	1.00
Preferred	−80.30	44.33	0.00	0.00	45.31	1.00

evaluation of extrinsic factors showed that home range size was inversely related to mean NDVI value and increased with distance to water. Our analytical approach also revealed statistical differences between males and females. Based on the estimates and confidence intervals of the model (Table S2) we found that home range size for females decreased with age, while age did not have a significant effect on male home range size. The hierarchical partitioning of the best model suggests that after sex, NDVI was the strongest predictor of home range size for southern mule deer (Fig. 2).

4. Discussion

Characterizing and understanding the factors that influence home range size and composition for vulnerable wildlife species is important, particularly in semi-arid landscapes like southern California where pressures on wildlife are intensifying through increased levels of urbanization, more frequent and intense fires, and droughts (Riley et al., 2003). For the southern mule deer, these pressures may mean limited access to resources in a semi-arid environment that is already water limited. We found that water and forage quality, which vary seasonally, are important to both home range size and selection of the southern mule deer. These factors, in combination with the intrinsic variables of sex and age, shape southern mule deer resource needs and space use.

4.1. Home range selection

Our analyses identified habitat characteristics associated with limited resources in each season. In the wet season, deer selected for areas with greater NDVI values and higher levels of precipitation, while avoiding areas with greater proximity to water sources. In the dry season however, both NDVI and precipitation were insignificant in resource selection functions, whereas deer selected for areas with a greater proximity to available water (Table 3). In the arid southwest, water sources are largely ephemeral, so it is very likely that in the dry season, when precipitation is either low or non-existent, deer are reliant on artificial water drinkers, moisture from vegetation, and the rare permanent streams that exist throughout their habitats. However, in the wet season when precipitation is high, deer shift their resource needs to areas with greater precipitation and better forage quality. In previous resource selection studies, NDVI was found to be a variable that is commonly selected for by large herbivores (Marshal et al., 2006a). However, our data from these semi-arid study sites show that water resources are more influential than forage quality on home range selection for southern mule deer in the dry season. These findings align with other mule deer studies in the arid southwest including California, Arizona, New Mexico, and Texas, where deer are typically found within 2.5 km of water sources, and water management has been beneficial to mule deer in the southwest (Severson and Medina, 1983). We also found no specific selection or avoidance of vegetation types between seasons, though there was a higher prevalence of some specific vegetation types. Selection of NDVI suggests that southern mule deer are opportunistic browsers rather than being dependent on a specific vegetation type. While there have been previous studies of the diet of the southern mule deer in this area, which found deer to favor juniper, riparian, and desert scrub habitats (Colby 2008), this was the first study that examined seasonal changes in habitat selection.

Home range characteristics that remained consistent between the wet and dry seasons for southern mule deer included an apparent avoidance of all road types and a preference for areas with higher CWD. Roads often act as barriers to many wildlife species, including deer (Nicholson et al., 1997), so road avoidance is likely the result from a strong barrier effect, which was captured more effectively with our use of the LoCoH home range estimation method. A visual inspection of southern mule deer LoCoH home range confirms this pattern (Fig. S1). The fact that deer appeared to select for areas with a higher CWD between both wet and dry seasons was unexpected. This result may seem counterintuitive, as areas with higher CWD represent areas of higher drought stress on both soils and plants. However, in semi-arid Mediterranean climates like southern California, CWD can act as a proxy for water demand for the soil and vegetation (Stephenson 1998). In chaparral habitats throughout southern California, many species of plants are adapted to grow in consistently dry conditions using strategies like having long deep roots (Hellmers et al., 1955). Both chamise and scrub oak vegetation, which southern mule deer have been found to favor in this region (Colby 2008), are species that are more deeply rooted and can persist in areas with higher CWD values.

Southern mule deer also consistently selected home ranges that avoided gentle slopes and higher elevations across seasons. These choices could reflect the animal's survival strategies as a prey species, often referred to as the 'landscape of fear' (Brown and Kotler 2004). Within the two-year period of this study, we identified 15 mortalities that we determined from necropsy were caused by external factors: five we attributed to vehicle collisions, and ten determined to be mountain lion kills. In the arid southwest where vegetative cover may be limited, deer and other prey animals often rely on topographic features, like steep slopes, to hide from predators. Other studies have also found that mule deer tend to more commonly bed and select for steeper landscapes when they are more vulnerable to predation (Marshal et al., 2006b) as this type of topography can provide greater concealment and cover from predators when compared to the exposure of gentler slopes. The avoidance of higher elevations is also likely related to a greater risk of predation in the exposed areas at higher elevations in comparison to the drainages, riparian habitats, and more vegetated areas at lower elevations which may offer more cover.

4.2. Home range size

We found that important drivers of seasonal home range selection in southern mule deer also influence home range size. Both forage quality, measured as NDVI (Marshal et al., 2006a), and water are limited resources in southern California, and we found both influenced deer home range size. From our models, NDVI had the second highest influence overall on home range size (Fig. 2), illustrating the importance of forage and landscape nutrition, rather than specific vegetation types, in southern mule deer habitat preferences. This result is expected as herbivores tend to select and forage opportunistically in areas that have new plant growth and higher nutritional quality (Marshal et al., 2006a). In areas with better forage quality, deer require less space to acquire the resources necessary to meet their energetic demands. Similarly, deer that had greater variation in the proximity to water within their home range had larger home ranges to support their water needs. Water is critical to animals living in arid environments and maintaining artificial water sources for the southern mule deer is likely very important to their survival.

Pairing intrinsic demographic variables with extrinsic environmental variables in the analysis of southern mule deer home range size allowed us to identify some of the underlying mechanisms driving resource needs and use in a resource-limited environment. We find that a combination of demographic (age and sex) and environmental (NDVI and water proximity) factors were the best predictors of home range, where sex appears to play the largest role in determining home range size in southern mule deer. This result is expected, as male mammals tend to have larger home ranges in order to maintain more reproductive opportunities (Aronsson et al., 2016). However, unlike other studies (McNab 1963; Harestad and Bunnel 1979; Lindstedt et al., 1986; Swihart et al., 1988) we did not find a significant influence of animal size on home range size. Our results do however show that older females tended to have smaller home ranges in comparison to younger females, while we found no difference in home range size among male age groups. The age range for males (3–6 years) in our study is significantly smaller than that among females (1–11 years), so we likely did not have the data available to detect a relationship between age and sex among male deer. The survival rate for male deer in our study was also lower than females (58.8% and 65% respectively), so various pressures like hunting and rut injuries may lessen the longevity of males over females. In regard to the decreased home range size in older female southern mule deer, it is possible that as females age, they may be honing and reducing space use to maximize resources while limiting energetic requirements to get to those resources, indicating the importance of maintaining high quality habitat for deer survival.

Our findings highlight the importance of understanding and evaluating both the intrinsic demographic and extrinsic environmental factors to assess an animal's habitat and space use. In the case of the southern mule deer, we found that an interaction between sex and age, as well as forage quality and water proximity are all vital factors in determining space use. This also suggests that seasonal variations in key environmental conditions and selection for changing resources are important to understanding how an animal interacts with its environment. This relationship may become more consequential in light of predictions of increased drought intensity and frequency (Diffenbaugh et al., 2015; Mann and Gleick 2015). For the southern mule deer, a harvested ungulate of conservation concern, maintaining water sources and forage quality within their habitat will likely be critical to conserving healthy populations with increased climate uncertainty.

CRediT authorship contribution statement

Field work was conceived and designed by E. T, M.J, R. B, and R.L. Statistical analyses were conducted by E. T, with input from M.J and R.L. The manuscript was written by E. T, M.J and R.L with all authors providing comments, edits and feedback on manuscript drafts.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

All funding for this reasearch was provided by the California Department of Fish and Wildlife.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2022.104728.

References

Akaike, H., 1973. Maximum likelihood identification of Gaussian autoregressive moving average models. Biometrika 60, 255–265. https://doi.org/10.1093/BIOMET.
Albon, S.D., Langvatn, R., 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos 65, 502. https://doi.org/10.2307/3545568.
Aronsson, M., Low, M., López-Bao, J.V., et al., 2016. Intensity of space use reveals conditional sex-specific effects of prey and conspecific density on home range size. Ecol. Evol. 6, 2957–2967. https://doi.org/10.1002/ece3.2032.
Bates, D., Maechler, M., Bolker, B., et al., 2019. Package "Lme4".
Bohonak, A.J., 2012. Social Structure and Genetic Connectivity in the Southern Mule Deer: Implications for Management This Is a Final Report for the Project "Social Structure and Genetic Connectivity in the Southern Mule Deer: Implications for Management" to Andrew J. Bohonak from California Department of Fish and Wildlife (CDFW).
Boone, R.B., Thirgood, S.J., Hopcraft, J.G.C., 2006. Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. Ecology 87.
Börger, L., Franconi, N., De Michele, G., et al., 2006. Effects of sampling regime on the mean and variance of home range size estimates. J. Anim. Ecol. 75, 1393–1405. https://doi.org/10.1111/j.1365-2656.2006.01164.x.
Brown, J.S., Kotler, B.P., 2004. Hazardous duty pay and the foraging cost of predation. Ecol. Lett. 7, 999–1014.
Burnham, K., Anderson, D., 1998. Practical Use of the Information-Theoretic Approach. Model Selection and Inference. Springer, New York, pp. 75–117.
Burt, W.H., 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24, 346. https://doi.org/10.2307/1374834.
Byrne, M.E., Clint McCoy, J., Hinton, J.W., et al., 2014. Using dynamic Brownian bridge movement modelling to measure temporal patterns of habitat selection. J. Anim. Ecol. 83, 1234–1243. https://doi.org/10.1111/1365-2656.12205.
Calenge, C., 2020. Package "adehabitatHR" - Home Range Estimation.
Cederlund, G., Sand, H., 1994. Home-range size in relation to age and sex in moose. J. Mammal. 75, 1005–1012. https://doi.org/10.2307/1382483.
Colby, J., 2008. Comparison of VHF and GPS data from radio-collared female mule deer. location error, home range attributes, and habitat selection.
Diffenbaugh, N.S., Swain, D.L., Touma, D., Lubchenco, J., 2015. Anthropogenic warming has increased drought risk in California. Proc. Natl. Acad. Sci. U. S. A. 112, 3931–3936. https://doi.org/10.1073/pnas.1422385112.
Erickson, J.A., Anderson, A.E., Medin, E., Bowden, D.C., 1970. Estimating ages of mule deer: an evaluation of technique accuracy. J. Wildl. Manag. 34, 523. https://doi.org/10.2307/3798857.
Fryxell, J.M., Hazell, M., Börger, L., et al., 2008. Multiple movement modes by large herbivores at multiple spatiotemporal scales. Proc. Natl. Acad. Sci. U. S. A. 105, 19114–19119. https://doi.org/10.1073/pnas.0801737105.
Gelman, A., 2008. Scaling regression inputs by dividing by two standard deviations. Stat Med Stat Med 27, 2865–2873. https://doi.org/10.1002/sim.3107.
Getz, W.M., Fortmann-Roe, S., Cross, P.C., et al., 2007. LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. PLoS One 2, e207. https://doi.org/10.1371/journal.pone.0000207.
Getz, W.M., Wilmers, C.C., 2004. A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. Ecography 27, 489–505. https://doi.org/10.1111/j.0906-7590.2004.03835.x.
Gilleland, E., 2015. Package "Smoothie" Title Two-Dimensional Field Smoothing.
Gompper, M.E., 2002. Top Carnivores in the Suburbs? Ecological and Conservation Issues Raised by Colonization of North-eastern North America by CoyotesThe expansion of the coyote's geographical range may broadly influence community structure, and rising coyote densities in the suburbs may alter how the general public views wildlife. Bioscience 52, 185–190. https://doi.org/10.1641/0006-3568(2002)052[0185:tcitse]2.0.co;2.
Harestad, A.S., Bunnel, F.L., 1979. Home range and body weight-A reevaluation. Ecology 60, 389–402. https://doi.org/10.2307/1937667.
Harris, S., Cresswell, W.J., Forde, P.G., et al., 1990. Home-range analysis using radio-tracking data–a review of problems and techniques particularly as applied to the study of mammals. Mamm Rev. 20, 97–123. https://doi.org/10.1111/j.1365-2907.1990.tb00106.x.
Hellmers, H., Horton, J.S., Juhren, G., O'keefe, J., 1955. Root Systems of Some Chaparral Plants in Southern California.
Hooten, M.B., Hanks, E.M., Johnson, D.S., Alldredge, M.W., 2014. Temporal variation and scale in movement-based resource selection functions. Stat. Methodol. 17, 82–98. https://doi.org/10.1016/j.stamet.2012.12.001.
Johnson, C.J., Nielsen, S.E., Merrill, E.H., et al., 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. J. Wildl. Manag. 70, 347–357. https://doi.org/10.2307/3803680.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65–71. https://doi.org/10.2307/1937156.

Kruskal, W.H., Wallis, W.A., 1952. Use of ranks in one-criterion variance analysis. J. Am. Stat. Assoc. 47, 583. https://doi.org/10.2307/2280779.

Lewis, M.A., Murray, J.D., 1993. Modelling territoriality and wolf-deer interactions. Nature 366, 738–740. https://doi.org/10.1038/366738a0.

Lindstedt, S.L., Miller, B.J., Buskirk, S.W., 1986. Home range, time, and body size in mammals. Ecology 67, 413–418. https://doi.org/10.2307/1938584.

Mann, M.E., Gleick, P.H., 2015. Climate change and California drought in the 21st century. Proc. Natl. Acad. Sci. U.S.A. 112, 3858–3859.

Marshal, J.P., Bleich, V.C., Krausman, P.R., et al., 2006a. Factors affecting habitat use and distribution of desert mule deer in an arid environment. Wildl. Soc. Bull. 34, 609–619. https://doi.org/10.2307/3784686.

Marshal, J.P., Lesicka, L.M., Bleich, V.C., et al., 2006b. Demography of desert mule deer in southeastern California. Calif. Fish Game 92, 55–66.

McKee, C.J., Stewart, K.M., Sedinger, J.S., et al., 2015. Spatial distributions and resource selection by mule deer in an arid environment: responses to provision of water. J. Arid Environ. 122, 76–84. https://doi.org/10.1016/j.jaridenv.2015.06.008.

McNab, B.K., 1963. Bioenergetics and the determination of home range size. Am. Nat. 97, 133–140. https://doi.org/10.1086/282264.

Nicholson, M.C., Bowyer, R.T., Kie, J.G., 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. J. Mammal. 78, 483–504. https://doi.org/10.2307/1382900.

Pérez-Solano, L.A., García-Feria, L.M., Gallina-Tessaro, S., 2017. Factors affecting the selection of and displacement within core areas by female mule deer (Odocoileus hemionus) in the Chihuahuan Desert, Mexico. Mamm. Biol. 87, 152–159. https://doi.org/10.1016/j.mambio.2017.08.005.

Powell, R.A., Mitchell, M.S., 2012. What is a home range? J. Mammal. 93, 948–958. https://doi.org/10.1644/11-mamm-s-177.1.

R Development Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Riley, S.P.D., Sauvajot, R.M., Fuller, T.K., et al., 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. Conserv. Biol. 17, 566–576. https://doi.org/10.1046/j.1523-1739.2003.01458.x.

Schwarz, G., 1978. Estimating the dimension of a model. Ann. Stat. 6, 461–464. https://doi.org/10.1214/AOS/1176344136.

Severson, Kieth E., Medina, Alvin L., Forest Service, US Department of Agriculture, 1983. The Santa Rita Experimental Range. Wildlife and Range Research Needs in Northern Mexico and Southwestern United States: Workshop Proceedings, April 20-24, 1981, Rio Rico, Arizona 36, 56.

Stephenson, N.L., 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. J. Biogeogr. 25, 855–870. https://doi.org/10.1046/j.1365-2699.1998.00233.x.

Swihart, R.K., Slade, N.A., Bergstrom, B.J., 1988. Relating body size to the rate of home range use in mammals. Ecology 69, 393–399. https://doi.org/10.2307/1940437.

Taber, R.D., Dasmann, R.F., 1958. The black-tailed deer of the chaparral: its life history and management in the north coast range of California. Game Bulletin No 8.

Tsalyuk, M., Kilian, W., Reineking, B., Getz, W.M., 2019. Temporal variation in resource selection of African elephants follows long-term variability in resource availability. Ecol. Monogr. 89, e01348 https://doi.org/10.1002/ecm.1348.

Tufto, J., Andersen, R., Linnell, J., 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. J. Anim. Ecol. 65, 715. https://doi.org/10.2307/5670.

Walsh, C., Mac Nally, R., 2020. Hierarchical Partitioning Package "hier.Part".

Walton, Z., Samelius, G., Odden, M., Willebrand, T., 2017. Variation in home range size of red foxes Vulpes vulpes along a gradient of productivity and human landscape alteration. PLoS One 12. https://doi.org/10.1371/journal.pone.0175291.

Wang, M., Grimm, V., 2007. Home range dynamics and population regulation: an individual-based model of the common shrew Sorex araneus. Ecol. Model. 205, 397–409. https://doi.org/10.1016/j.ecolmodel.2007.03.003.

Zuur, A.F., Ieno, E.N., Walker, N.J., et al., 2009. Mixed Effects Models and Extensions in Ecology with R.