ECOLOGICAL AND SOCIAL DRIVERS OF MEXICAN GRAY WOLF (*CANIS LUPUS BAILEYI*) HOME RANGE PATTERNS ACROSS SPATIOTEMPORAL SCALES

By

Evelyn Marie Lichwa

A Thesis Presented to

The Faculty of Humboldt State University

In Partial Fulfillment of the Requirements for the Degree

Master of Science in Natural Resources: Wildlife

Committee Membership

Dr. Micaela Szykman Gunther, Committee Chair

Dr. Ho Yi Wan, Committee Member

Dr. James W. Cain III, Committee Member

Dr. Erin Kelly, Program Graduate Coordinator

December 2021

ABSTRACT

ECOLOGICAL AND SOCIAL DRIVERS OF MEXICAN GRAY WOLF (*CANIS LUPUS BAILEYI*) HOME RANGE PATTERNS ACROSS SPATIOTEMPORAL SCALES

Evelyn Marie Lichwa

Elucidating factors influencing home range size are fundamental relationships that can be described for any wildlife species, particularly those of conservation concern. The Mexican gray wolf (*Canis lupus baileyi*) is an endangered sub-species of the gray wolf whose home range patterns have not yet been studied. I estimated home range sizes for 22 Mexican wolf packs using Brownian Bridge Movement Models (95% UD). Generalized linear mixed effect models were used to evaluate environmental and social variables across four timeframes. Annual home range size was inversely related to human density and tree cover. During the denning period, home range was inversely related to litter size and increased with pack size. Post denning home range was inversely related to ungulate biomass and positively related to pack size. During the non-denning season, home range was inversely correlated with snow depth. Results found herein both confirm as well as deviate from results found in other wolf populations, notably, the inverse correlation with pack size at the annual scale, but positive correlation at seasonal timeframes. The opposite relationships with home range and pack size, and the significance of ungulate biomass at the seasonal scale but not the annual scale demonstrates the importance of evaluating factors influencing home range using a

multiscale approach as home range size may be differentially influenced by the same variable across timescales. Thus, future home range studies should use a multiscale approach to discern relevant factors for species across timeframes of interest.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Elucidating the relationship between wildlife movements and their ecological and social environment can provide important information for conserving and managing species and populations, particularly those of conservation concern (Miller et al. 2017). Home range is a central focus when measuring wildlife movement (Nathan et al. 2008). It represents the relationship between the environment and an individual's understanding of that environment (Powell and Mitchell 2012) and can be viewed as a trade-off between resource access and energetic costs (Mattisson et al. 2013). Interactions between wildlife behavior and the environment provide insight into patterns that are often characterized using home range size (Börger et al. 2006).

Home range size, and the factors influencing it, are fundamental ecological parameters for describing species-environment relationships. Estimates of home range size have been used for designing protected areas for wildlife (Gosling et al. 2000), as a tool for obtaining estimates of population size (Gros et al. 1996), and as a proxy for local density in an area, especially in territorial species (Mattisson et al. 2013). Elucidating variation in home range size can assist in predicting a species' space use or density in new areas (Herfindal et al. 2005). This can be particularly important for species that roam extensively and experience human-wildlife conflict (Woodroffe et al. 2005) and is likely important to recovering populations whose range may expand into new areas.

Home range size in mammals is influenced by both ecological and social factors. Food biomass and availability represent important ecological factors that are typically

inversely related to home range size both in herbivores (e.g., wallaby (*Onychogalea fraenata*), Fisher 2000; elk (*Cervus elaphus*), Anderson et al. 2005; moose (*Alces alces*), van Beest et al. 2011) and carnivore species (e.g., African lions (*Panthera leo*), Loveridge et al. 2009; tigers (*Panthera tigris*), Simchareon et al. 2014; coyotes (*Canis latrans*), Ward et al. 2018). Climatic factors such as temperature and snow depth are other ecological factors that influence home range size in mammals. For example, home ranges of bobcats (*Lynx rufus*) in Idaho were restricted by snow resulting in winter home ranges that were almost four times smaller than summer home ranges due to increased energetic costs (Koehler and Hornocker 1989). Conversely, home range size of female elk increased as a result of snow depth in Yellowstone National Park due to forage being scarce and covered by snow (Anderson et al. 2005). With respect to temperature effects on animal movement, in a study of African wild dogs (*Lycaon pictus*), higher ambient temperature resulted in reduced daily distance traveled (Pomilia et al. 2015), and in red foxes (*Vulpes vulpes*), home range size was positively correlated with higher mean temperature, possibly due to seasonal fluctuations in food abundance (Main et al. 2020).

In addition to ecological factors, social factors are also important variables shaping home range size. In a study of Ethiopian wolves (*Canis simensis*), home range size increased with pack size (Ashenafi et al. 2005), while pack size accounted for 87% of variation in home range size in coyotes (Bowen 1981), and litter size was the most influential driver of seasonal home range size in a study of African wild dogs where larger litters correlated with smaller home ranges (Pomilia et al. 2015). Intraspecific

variation in determinants of home range size has also been documented in gray wolf

(*Canis lupus*) populations.

Wolves are an extensively studied and wide-ranging species; as a result, there is a

robust understanding of factors influencing gray wolf home range size (see review:

Jedrzejewski et al. 2007). Wolf home range size has been negatively correlated with prey

biomass, wolf density, and pack size, and positively correlated with latitude, elevation,

and human density (Ballard et al 1987, Wydeven et al. 1995, Okarma et al. 1998,

Jedrzejewski 2007, Fuller et al. 2010, Rich et al. 2012, Mattisson et al. 2013). However,

studies from different regions show conflicting results. Home range size in wolves has

been both positively (Guassa, Ethiopia; Ashenafi et al. 2005) and negatively (Montana,

United States; Rich et al. 2012) related to pack size; influenced by (Finland; Jedrzejewski

2007, Rich et al. 2012) and independent of (Scandinavia; Mattisson et al. 2013) prey

biomass; and influenced by (Poland; Mysłajek et al. 2018), and independent of

(Mattisson et al. 2013) wolf density. Furthermore, there is a paucity of research on

climatic variables influencing wolf home range size, although snow depth has been

recorded to reduce wolf movements (Alberta, Canada; Droghini and Boutin 2018a), tree

cover has been important in wolf home range selection at annual and seasonal timeframes

(Rocky Mountains, United States; Trapp et al. 2008, Wisconsin and Minnesota, United

States; Unger et al. 2009), and elevation has been important in denning home range

selection (Alaska; Joly et al. 2017).

Inconsistencies in results between studies suggest variables causing variation in

home range between and within gray wolf populations may not be fully understood

(Fritts and Mech 1981, Hayes and Harestad 2000, Gurarie et al. 2011, Rich et al. 2012, Mysłajek et al. 2018). Elucidating factors influencing variation in ranging patterns is important for any species, and perhaps particularly relevant for endangered species and species that experience high levels of human conflict (Woodroffe 2011, Morehouse and Boyce 2017).

The Mexican gray wolf (*Canis lupus baileyi*; hereafter: Mexican wolf) is an endangered sub-species of the gray wolf whose home range patterns have not been explicitly studied. Mexican wolves were extirpated from the wild by 1970 as a result of predator eradication efforts primarily to prevent livestock loss (Bednarz 1988, Brown and Shaw 2002). In 1976, the Mexican wolf was listed as endangered under the U.S. Endangered Species Act (ESA; USFWS 2017). After ESA listing, the remaining wild individuals were captured and placed in captivity to initiate the captive breeding program (McBride 1980). In 1998, Mexican wolves began to be reintroduced into Arizona's Apache-Sitgreaves National Forest. There are now at least 186 Mexican wolves within the Mexican Wolf Experimental Population Area (MWEPA; USFWS 2021), which is located across the states of Arizona and New Mexico. The White Mountain Apache Tribe, U.S. Fish and Wildlife Service (USFWS), Arizona Game and Fish Department (AZGFD), U.S. Forest Service (USFS), New Mexico Department of Game and Fish (NMDGF), and U.S. Wildlife Services (USWS) work collaboratively on the Mexican wolf recovery program and are collectively referred to as the Mexican Wolf Interagency Field Team (IFT). Previous Mexican wolf studies have evaluated conflict with livestock (Amirkhiz et al. 2018), habitat suitability (Martinez-Meyer et al. 2021), diet composition

(Reed et al. 2006), and genetics (Asa et al. 2007), but have yet to assess Mexican wolf ranging patterns and the factors influencing these patterns.

The goal of this study was to analyze ecological and social factors driving home range size of Mexican wolves. Home ranges were analyzed at two timescales: annual and seasonal (referred to collectively as timeframes). The seasons of biological significance included denning (pack movements constrained by young pups), post denning (pack traveling with older pups and at maximum size), and non-denning periods (peak timing of juvenile dispersal and breeding). Incidentally, these seasons also correspond to actions taken by the IFT to manage Mexican wolves. During the denning season, IFT conducts cross-fostering, which is when captive born Mexican wolf pups are transferred into wild dens to bolster genetics of the wild population. During post-denning, IFT conducts foothold trapping to capture and collar wolves for monitoring. During the non-denning season, the IFT conducts aerial darting, capture, and collaring as part of the annual population count.

Factors reported to influence home range size in gray wolves have been inconsistent between and within populations. Even so, it is currently assumed that Mexican wolf ranging patterns are influenced by the same factors and assumed to display similar patterns as other gray wolf populations (USFWS 2017). However, free ranging Mexican wolf life history and ecology were not systematically studied before extirpation from the wild. Therefore, this is the first study to assess factors influencing Mexican wolf home range size at annual and seasonal timescales and will provide new information on specific factors that affect Mexican wolf ranging patterns. Mexican wolf home range

sizes may be differentially influenced by multiple factors at different timescales due to varying resource needs during seasonal changes in pack dynamics, behavior, and caring for young. Thus, a multiscale approach is critical for understanding spatiotemporal variation in Mexican wolf ranging patterns and should be useful to their conservation and management.

Predictions

In accordance with previous research, I predicted that both ecological and social factors would be influential in determining Mexican wolf home range size at all timeframes. Specifically, I predicted home range size would be positively correlated with human density, and inversely correlated with tree cover, ungulate biomass, pack size, and wolf density at the annual timescale. During the denning season, I predicted that home range size would be positively correlated with elevation, but that denning home range size would decrease with increasing tree cover, ungulate biomass, litter, and pack size. I predicted a positive correlation between home range size and elevation, and an inverse correlation with tree cover, ungulate biomass, and pack size during the post denning period. Lastly, I predicted that during the non-denning period, home range size would positively correlate with elevation, and that home range size would be inversely correlated with snow depth, tree cover, ungulate biomass, and pack size.

MATERIALS AND METHODS

Study Area

The MWEPA begins from the western edge of the Arizona state line to the eastern edge of the New Mexico state line, extending south of Interstate 40 to the Mexico border and is comprised of three Mexican wolf management zones. The study area was wolf management Zone 1, which includes all the Gila, Apache-Sitgreaves National Forests; the Payson, Pleasant Valley and Tonto Basin Ranger Districts of the Tonto National Forest; and the Magdalena Ranger District of the Cibola National Forest (Fig. 1; USFWS 2017). Elevation in Zone 1 ranges from 501 to 3,480 m. Vegetation types in Zone 1 differ considerably across the MWEPA: lower elevation areas of southern Arizona and New Mexico are desert, comprised of creosote bush (*Larrea tridentata*) and succulent species (e.g., *Agave* spp., *Opuntia* spp.); between 900-1,200 m are woodlands dominated by junipers (*Juniperus* spp.), pinyon (*Pinus* spp.), and oaks (*Quercus* spp.); beginning around 1,500 m, the dominant vegetation is comprised of ponderosa pine (*Pinus ponderosa*), and as elevation increases so does the occurrence of Douglas fir (*Pseudotsuga menziesii*), true firs (*Abies* spp.), and spruce (*Picea* spp.) (USFWS 2017). Land ownership is also diverse; 43.5% of the MWEPA is managed by federal agencies; state agencies manage 15.3%, Tribal 9.9%, and private land comprises 31.30% (USFWS 2017). Other potentially competing species include black bears (*Ursus americanus*), mountain lions (*Puma concolor*), and coyotes (*Canis latrans*).
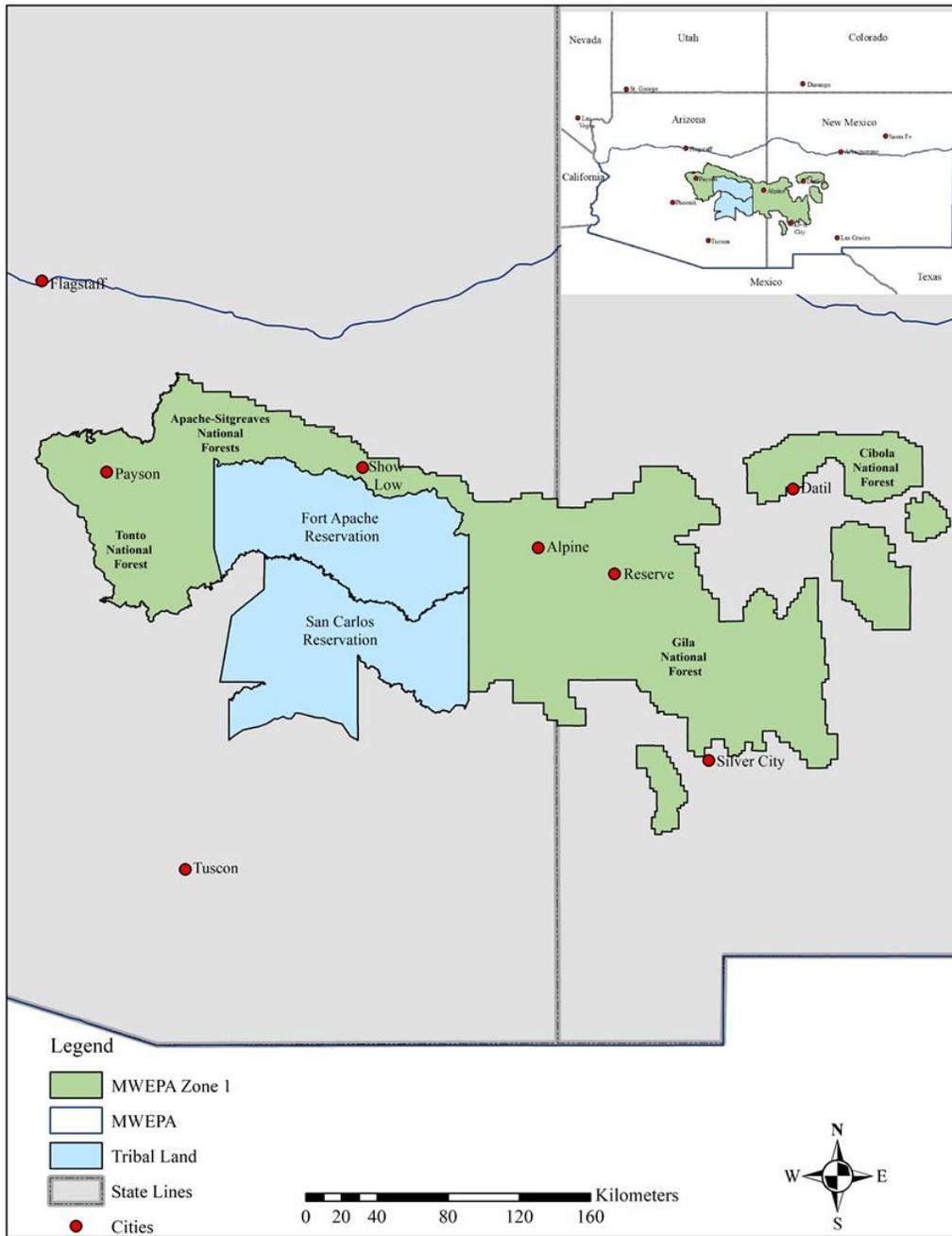
Figure 1. Mexican Wolf Experimental Population Area (MWEPA) boundaries including Zone 1 (study area) outlined in black and entire extent of the Mexican Wolf Experimental Population Area outlined in blue.

Pack Selection and Representation

Mexican wolf packs were selected based on established packs that maintained at least one member of the breeding pair wearing a GPS collar for at least one year between 1 April 2017 - 31 March 2021. Established packs were targeted because they were expected to utilize their range more efficiently compared to singles or new pairs by having accumulated knowledge of prey movements within their range, for example (Pomilia et al. 2015). The breeding pair, together, establish and maintain territories (Mech and Boitani 2003), and is expected to lead the pack to obtain necessary food and other resources with better knowledge of the environment than younger pack members. Data from a single collared breeding male or female wolf from each pack were used to estimate home range size within timeframes (similar to: Ciucci et al. 1997, Benson and Patterson 2014, Mancinelli et al. 2018).

Home Range Estimation

Methodological Considerations

There are many types of home range estimators available to evaluate an animal's space use. There is likely no single best home range estimator, and the choice of home range estimator should be chosen to address one's specific research questions (Powell and Mitchell 2012). I considered three different home range estimators based on previous wolf studies and current IFT management practices. These were minimum convex

polygon (MCP), kernel density estimator (KDE) using the reference bandwidth (h_{ref})

(currently used by IFT), and Brownian bridge movement model (BBMM).

MCP may be the most prevalent home range estimator used in wolf studies and is

one of the simpler estimations to calculate. MCP creates a home range polygon by

connecting the outermost points and generating the smallest convex polygon around the

points (Mohr 1947, Hayne 1949). MCP's disadvantage is that it often overestimates space

use, especially in species associated with large home ranges (Douglas-Hamilton et al.

2005). Further, the polygon estimate produced by MCP is not based on probability of

space use. Although still prevalent in the literature, MCP is well documented as no longer

being most suitable for estimating home range, with the advent of better methods (Börger

et al. 2006).

KDE is regarded as a better estimator as it incorporates a probabilistic model, and

therefore results in a more accurate home range estimate than MCP (Worton 1989,

Börger et al. 2006). However, KDEs are statistically biased, and assume location points

are independently and identically distributed in probability, and thus, does not account for

spatial or temporal autocorrelation of GPS points (Noonan et al. 2018). Spatial or

temporal autocorrelation can be remedied with KDE by subsampling data; the caveat to

subsampling one's data is that it removes pertinent information from home range

estimation because animals do not move randomly (Del Solla et al. 1999). Additionally,

KDE, especially with h_{ref}, has consistently been linked to overestimating home ranges

(Kie 2013, Fletcher and Fortin 2019).

Brownian bridge movement model improves on non-independence of GPS locations by estimating use between successive locations via a random-walk process from the time and distance between locations (Fletcher and Fortin 2019). In addition, BBMM uses the Brownian motion variance, which estimates the probability of the individual occurring in an area during a given period of time (Horne et al. 2007). BBMM uses the time of GPS locations and animal specific parameters including collar error and animal speed, which has proven to be more reliable than those home range estimators that do not have these parameters (Walter et al. 2015). Most importantly, and unlike KDE methods, BBMM does not assume that GPS locations are independent (Fletcher and Fortin 2019). Due to the pros and cons among the home range estimators in consideration, I selected BBMM as the home range estimator for this study.

Home Range Estimation

Mexican wolf GPS location data were used to estimate home range at two biological timescales: annually and during three biological seasons. Annual home ranges were estimated from locations collected starting on 1 April through 31 March of the following year as most pups were born in April. Biological seasons were based on data provided by IFT on timing of reproductive events and divided into: denning, corresponding to the period of time with young pups in the den and at rendezvous sites, 1 April – 31 July; post denning, when packs are traveling with pups and at maximum size, 1 August - 30 November; and non-denning, during peak dispersal and breeding time, 1 December - 31 March (IFT pers. comm. 2020, and similar to: Kunkel and Pletscher 2001, Smith et al. 2004, Houle et al. 2010, Mancinelli et al. 2018). GPS collar fixes from 2-4

points a day were included, and only data from one wolf were used at a time. After

separating the location data into the appropriate timeframes, data were brought into the

statistical program R for home range estimation with the package adehabitatHR (Calenge

2015). BBMM requires two smoothing parameters for home range estimation: 1) the

Brownian motion variance (σ_1), which sets the animals speed, and 2) the GPS error (σ_2),

which was set to 20 m (Mancinelli et al. 2018). I estimated the first smoothing parameter

using the R function *liker* in the adehabitatHR R package (Calenge 2006, Mancinelli et

al. 2018). Annual and seasonal home ranges were estimated using a 95% utilization

distribution (UD) isopleth, as that is typically considered the total range, and the same

isopleth across timeframes allowed for home range size comparison. If any outliers are

identified they will be kept in analyses since it represents real biological variability.

There was concern that data from a breeding female's collar may not be a good

representation of an entire pack's home range during the denning period as she is

suspected to stay closer to the den more often to care for pups. To alleviate this concern,

a paired t-test was conducted comparing home range sizes of each member of a breeding

pair across timeframes to ascertain if there was any significant difference between them

when both were collared in a pack.

Generalized Linear Mixed Effect Model Statistical Analyses

Generalized and linear mixed effect models (GLMM) are an extension of

traditional generalized linear models, that has been steadily increasing in popularity over

the last decade due to its ability to fit both fixed and random effects (Zuur et al. 2009,

Harrison et al. 2018). Fixed effects are variables that are hypothesized to influence the response variable (synonymous with covariates from traditional generalized linear models), and random effects typically relate to a grouping variable (e.g., packs within a population) that can control for and estimate the amount of variance from the random effect in the dataset (Zuur et al. 2009, Zuur and Ieno 2016, Harrison et al. 2018). There is no standardized protocol for which variables should be set as fixed or random, as it depends on the research questions. I chose GLMM for this analysis as the data set was biologically complex and benefitted from being able to fit both fixed and random effects.

Mixed effect models have been used to evaluate factors influencing home range size in various mammal species for over a decade, including for ungulates (e.g., roe deer, Börger et al. 2006; red deer, Rivrud et al. 2010; moose, van Beest et al. 2011; African buffalo (*Syncerus caffer*), Naidoo et al. 2012), canids (gray wolf, Mattisson et al. 2013; African wild dog, Pomilia et al. 2015; gray wolf, Mancinelli et al, 2018), and felids (jaguars (*Panthera onca*), ocelot (*Leopardus pardalis*), cougar, Figueira Machado et al. 2017).

To examine factors influencing Mexican wolf home range size during different timeframes, I employed generalized linear mixed effect models in the R library "lme4" (Bates et al. 2015), similar to other studies on pack-living canids (Mattisson et al. 2013, Pomilia et al. 2015, Mancinelli et al. 2018). Home range size (in km^2) was fitted as the response variable in all models. To ascertain the estimated significance of fixed effects (p-values) in final models the R package "lmerTest" was employed (Luke 2017).

Model Fixed Effects

Elevation (m above sea level) and percent tree cover (30 x 30 m resolution) for 2019 were acquired through the Land Fire and Resource Management Planning Tools program and downloaded from "Download Mosaic Data Products" of the land fire website (DMDP 2021). Human population density was acquired from the Gridded Population of the World, ver. 4.11 (CIESIN 2018) raster map at 1 km resolution. Daily measurements for snow depth (cm) for each non-denning season came from the Snow Data Assimilation System (SNODAS; NSIDC 2003), which is remotely sensed data collected and interpolated by the National Oceanic and Atmospheric Administration's (NOAA). The 2019 existing vegetation cover (EVC) reflects change and disturbance since the 2016 vegetation cover layer. This new layer includes vegetation cover and disturbance for the years 2017, 2018, and 2019. To get the tree cover within each home range (annual and seasonal), the EVC layer was clipped to each home range, and the resulting raster from the clip output was exported and run through the R library landscapemetrics (Hesselbarth et al. 2019) to get the percent of tree canopy cover within each home range.

The ungulate biomass index layer (0.01 x 0.01 m resolution) was developed from prey densities estimated by aerial surveys of elk, mule deer (*Odocoileus hemionus*), and white-tailed deer (*Odocoileus virginianus*; Martinez-Meyer et al. 2021). This layer represents the first spatial layer to display relative prey biomass available to Mexican wolves and was suitable for use in this study as Mexican wolves have been recorded to consume the ungulate species identified within the layer; wolf diet composition from scat

included 72.8% elk and 15.8% other prey including mule and white-tailed deer (Reed et

al. 2006). The ungulate biomass index (hereafter referred to as ungulate biomass; by km^2)

layer for the entire range of Mexican wolves was developed by Martinez-Meyer et al.

(2021) and acquired through CyVerse Data Commons (CyVerse 2020). Litter and pack

size for each season were obtained through IFT records. Wolf density was calculated at

the time of the annual population count in January of each study year with the total

number of individual wolves by the size (km^2) of their occupied range estimated by the

IFT.

Raster data for elevation, human density, snow depth, percent tree cover, and

ungulate biomass were brought into R and extracted by each home range polygon using

the *raster::extract()* function in the R library raster to get the average value per fixed

effect in each home range shapefile. All fixed effects were centralized and standardized

to improve model performance and interpretability, and to facilitate interpretation of the

relative strength of fixed effect estimates (Harrison et al. 2018). Standardizing the fixed

effects was done by subtracting the mean and dividing by the standard deviation giving

each fixed effect a mean of zero and a standard deviation of one. Fixed effects in

candidate models were checked for collinearity using Pearson's correlation and for

multicollinearity using the variance inflation factor (VIF).

Model Random Effect

"PackID" was set as a random effect to account for patterns in the residuals of the

fixed effects due to repeated observations of packs (Mattisson et al. 2013, Pomilia et al.

2015, Mancinelli et al. 2018). Further, designating pack as a random effect allowed

comparison with other similar studies as well as application of results to the rest of the

Mexican wolf population (Harrison et al. 2018).

<u>Preliminary Analyses</u>

Year was set as both a fixed and random effect in preliminary models to test for

significance and variance explained. As the data spanned 4 years, the variable year was

tested for significance to support combining all years of data for each timeframe into one

analysis and for amount of variance to see if it should be included as a random effect.

Food caching is a management technique that supplements food to packs to divert

the activity of Mexican wolves away from human-wildlife conflict over livestock or

supplement packs that were given additional pups to take care of via cross fostering.

Food caching schedules and intensity (how much food and how frequent) varied between

pack and season. Providing supplemental food to packs may influence home range size;

thus, food caching was included in preliminary models to evaluate whether it should be

included as a fixed or random effect and was denoted as "0" for not being food cached

during that timeframe and a "1" if that pack was food cached during that timeframe.

<u>Model Selection and Validation</u>

For each timeframe, I fit a global model with a combination of the following

standardized fixed effects: elevation, human density, snow depth, percent tree cover,

ungulate biomass, litter size, pack size, and wolf density. For each global model (one for

each timeframe), the "dredge" command in the R library "MuMIn" was used to evaluate

all possible combinations of fixed effects to develop candidate models based on AICc

(Akaike Information Criterion adjusted for small sample size) values and select the most

parsimonious model (Mattisson et al. 2013, Pomilia et al. 2015, Mancinelli et al. 2018).

Dredge is a reasonable model selection tool in this research; the selected fixed effects

affected wolf home range size in other systems. Models were listed by ΔAICc, and the

most parsimonious model was selected.

While using AIC is useful for selecting the most parsimonious model and

evaluating relative fit between a set of candidate models, AIC does not tell us about the

absolute model fit (Burnham and Anderson 2002, Nakagawa and Schielzeth 2013). To

assess goodness-of-fit of the fixed effects and entire mixed model, I used the R function

r.squaredGLMM() in the library MuMIn to obtain the marginal R^2 and conditional R^2

values for each final model. The marginal R^2 assesses the variance explained by the fixed

effects and the conditional R^2 assesses the variance explained by both fixed and random

effects (i.e., the variance explained by the entire model; Nakagawa and Schielzeth 2013).

RESULTS

Home Range Representation and Size Estimation

Twelve Mexican wolf packs contained a breeding pair collared together during the same time period. No significant differences in home range size were found among timeframes between individuals of the breeding pair (annual: t_5=-1.14, $p = 0.30$; denning: $t_5 = -0.65$, $p = 0.54$; post denning: $t_5 = -1.31$, $p = 0.24$; non-denning: $t_5 = -0.44$, $p = 0.67$.) Therefore, it was appropriate to use location data for packs from one member of the breeding pair. This resulted in a total of 22 wolf packs represented by 24 individual wolves available for analysis: 11 packs from Arizona (Pack ID: Bear Wallow, Hoodoo, Panther Creek, Elk Horn, Pine Spring, Prime Canyon, Saffel, Sierra Blanca, Rocky Prairie, Castle Rock, Eagle Creek) and 11 packs from New Mexico (Pack ID: Lava, Leopold, Luna, Mangas, Prieto, Sheepherders Baseball Park, Frieborn, Iron Creek, San Mateo, Colibri, Pitchfork Canyon; Fig. 2).
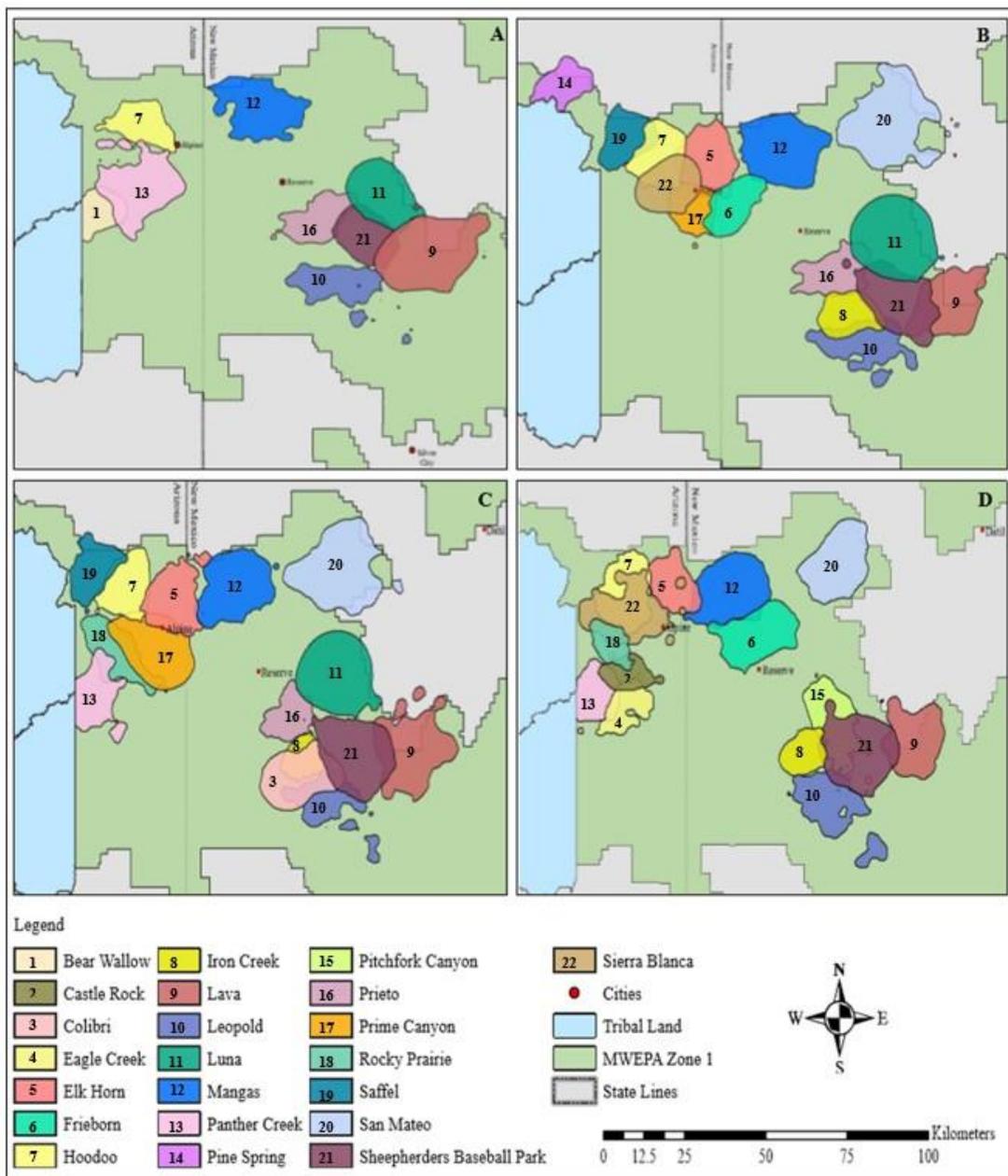
Figure 2. Distribution of annual home ranges for 22 Mexican wolf packs in the MWEPA Zone 1 between 1 April 2017 and 31 March 2021. Panels represent annual distribution of packs for 2017 (A), 2018 (B), 2019 (C), and 2020 (D). Home ranges were clipped at tribal land boundaries.

In total, 43,822 GPS location were recorded, yielding 216 home ranges (54 for each season: annual, denning, post denning, non-denning) estimated with 95% UD Brownian Bridge Movement Model for 22 Mexican wolf packs over a period of 4 years and 4 timeframes (Table 1, Appendix A). Three packs were removed from the denning season analysis since they did not have a litter. Across the study period, annual home range size averaged 446 km^2 (range: 174-860 km^2); denning: 234 km^2 (range: 34-920 km^2); post denning: 373 km^2 (range: 120-1,892 km^2); and non-denning: 518 km^2 (range: 162-1,722 km^2; Table 1). Denning home range size contracted to 47% of annual home range size; post denning size contracted 15% from annual size and increased 59% from denning size; and non-denning home range size was 14% larger than the annual home range size and 35% larger than post denning size (Fig. 3).

Table 1. Average home range sizes (km^2) per year and timeframe as estimated using Brownian Bridge Movement Model (BBMM) 95% UD for 22 Mexican wolf packs by year and timeframe in the MWEPA Zone 1, United States.

Primary Year	Annual	Denning	Post Denning	Non-Denning
2017	477	243	347	640
2018	436	186	370	523
2019	471	238	340	508
2020	402	274	425	401
All Years	446	234	373	518
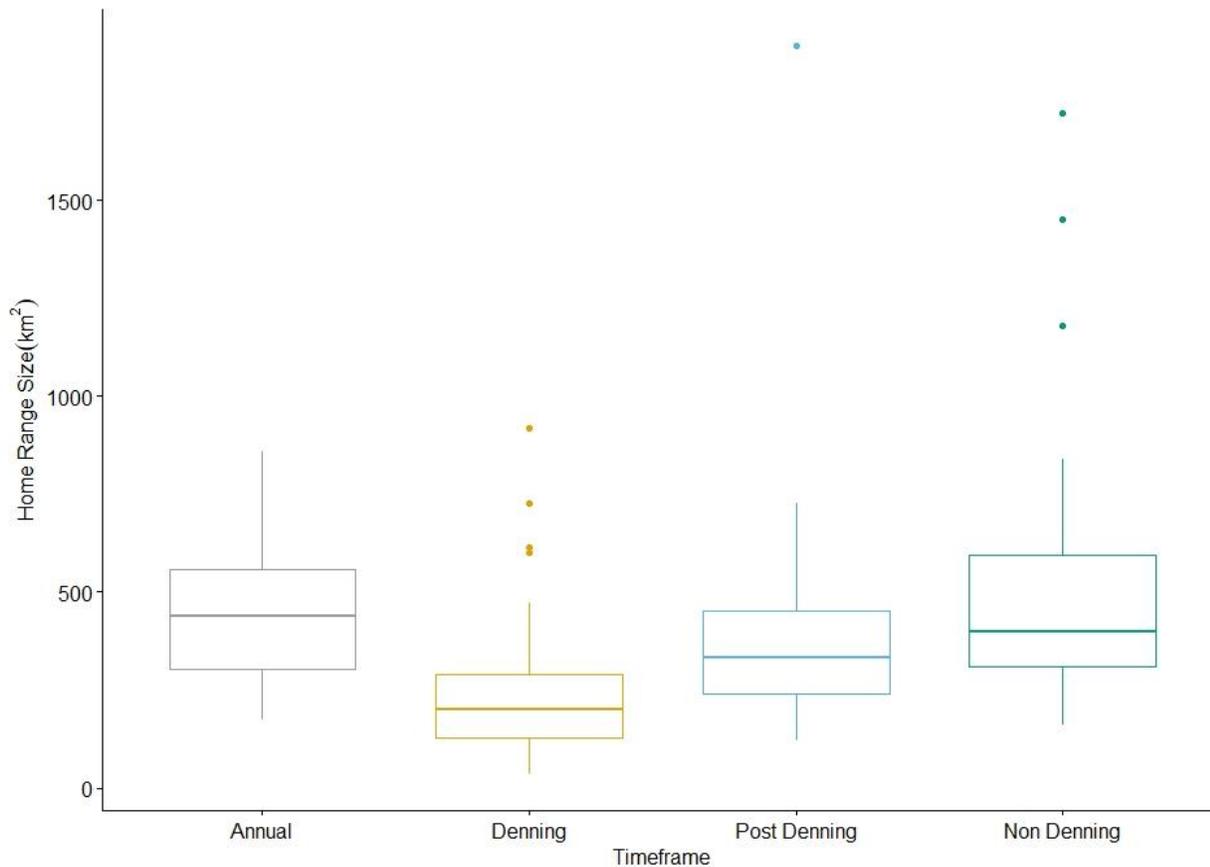
Figure 3. Boxplots demonstrating Mexican wolf home range size fluctuation throughout the 4 timeframes for 22 packs. Boxes represent the interquartile range, the thin lines in the middle represent the median, and dots indicate outliers.

Home Range Patterns

Ecological variables of elevation, human density, tree cover, snow depth, and ungulate biomass did not vary much between timeframes (Table 2). The social variables of litter and pack size showed more variation across time periods than the ecological variables. Across the study period, average litter size was 5 pups (Table 2). Pack size increased by 75% from the denning to the post denning period and then decreased by 28% into the non-denning period. The annual density of wolves did not change much between the years 2017-2021 (Table 2).

Table 2. Average and range (in parentheses) of ecological and social variables influencing Mexican wolf home ranges across 4 timeframes and 4 years in the MWEPA Zone 1, United States. -- denotes no value for that variable at that timeframe.

Variable	Annual	Denning	Post Denning	Non-Denning
Elevation (m)	--	2,481	2,484	2,424
		(2,182-2,761)	(2,209-2,720)	(2,149-2,646)
Human Density	0.27	--	--	--
(per 1 km)	(0.00-1.65)			
Snow Depth (cm)	--	--	--	28.25
				(3-75)
Tree Cover (%)	76.46	75.69	76.04	77.40
	(49-96)	(37-96)	(45-95)	(51-95)
Ungulate Biomass	0.81	0.83	0.82	0.80
(per km^2)	(0.62-0.92)	(0.55-0.93)	(0.62-0.92)	(0.58-0.92)
Litter Size	--	5	--	--
		(1-11)		
Pack Size	6	4	7	5
	(2-10)	(2-7)	(2-13)	(2-11)
Wolf Density (per	0.003	--	--	--
km^2)	(0.002-0.004)			

Generalized Linear Mixed Effect Models

Preliminary Analysis

Year was not significant in shaping home range size during any season, and R^2 values explained <5% of variation across timeframes (annual 0.4%; denning 0.06%; post denning 1%; and non-denning 4.9%). Therefore, year was neither included as a fixed nor random effect and data were pooled across years. Similarly, food caching did not show significantly different effects in shaping home range size (p values: denning 0.09; post denning 0.97; and non-denning 0.75), and R^2 values explained <2% of variation across seasons (denning 1.7%; post denning 0.4%; and non-denning 1.6%) and thus was not included in seasonal models as a fixed or random effect.

Model Selection

Fixed effects evaluated in all models were not correlated; Pearson's correlation (ɤ) values were <0.6 and checked for multicollinearity using the variance inflation factor, with all VIF values <5 (Zuur et al. 2009). The annual timescale was fit with a global model of human density, tree cover, ungulate biomass, pack size, and wolf density. The model selection output produced 32 models for evaluation, where the top model at this timescale was the global model (Table 3).

The denning period was fit with a global model of elevation, tree cover, ungulate biomass, litter size, and pack size. The model selection output yielded 16 models for evaluation where the top model excluded the fixed effect of elevation but retained tree cover, ungulate biomass, litter size, and pack size (Table 3). The global model for the

post denning period was elevation, tree cover, ungulate biomass, and pack size. The

model selection output yielded 8 models, with the top model including tree cover,

ungulate biomass, and pack size (Table 3).

The non-denning period was fit with a global model of elevation, snow depth, tree

cover, ungulate biomass, and pack size. Sixteen models were evaluated from the dredge

output, with the final model retaining snow depth, tree cover, ungulate biomass, and pack

size (Table 3). The top three models were included for all timeframes.

Table 3. Model selection table for evaluating factors influencing Mexican wolf home
range size during annual and seasonal timescale in Arizona and New Mexico
between 1 April 2017 and 31 March 2021, ranked using AIC corrected for small
sample size (AIC_c). K represents the number of fixed effects and w each model's
weight. Fixed effect abbreviations are E = elevation, HD = human density, SD =
snow depth, TC = tree cover, UBI = ungulate biomass, LS= litter size, PS = pack
size, and WD = wolf density.

Timeframe	Candidate Models	K	AIC_c	ΔAIC_c	w
Annual	HD + TC + UBI + PS + WD	5	657.4	0.00	0.79
	HD + TC + UBI + PS	4	662.5	5.04	0.06
	HD + TC + UBI + WD	4	663.1	5.63	0.04
Denning	TC + UBI + LS + PS	4	576.0	0.00	0.46
	UBI + LS + PS	3	577.5	2.53	0.11
	E + TC + UBI + LS + PS	5	578.9	6.02	0.06
Post Denning	TC + UBI + PS	3	710.9	0.00	0.75
	E + TC + UBI + PS	4	713.5	2.65	0.20
	UBI + PS	2	718.3	7.47	0.01
Non-Denning	SD + TC + UBI + PS	4	725.6	0.00	0.55
	E + SD + TC + UBI + PS	5	726.4	0.78	0.37
	SD + TC + UBI	3	732.4	6.72	0.01

Generalized Linear Mixed Effect Model Results

At the annual timescale, human density, tree cover, and pack size were negatively

correlated with home range size (Table 4, Fig. 4). According to the top model estimates,

Ungulate biomass was the strongest variable explaining home range size (β=-40.34,

Table 4), although not significant, followed by human density (β=-29.51, Table 4).

Ungulate biomass and wolf density were not found to be influential in this data set at this

timescale. The fixed effects explained 43% of the variation in data while the entire model

(fixed and random effects) explained 87% of the variation in data which results in packs

accounting for 44% of variability at the annual timeframe.

Table 4. Final model parameters and results for evaluating ecological and social
determinants of Mexican wolf home range size over 4 years and 4 timeframes in
the MWEPA Zone 1 of Arizona and New Mexico, USA using generalized linear
mixed effect models. Fixed effect abbreviations are HD = human density, SD =
snow depth, TC = tree cover, UBI = ungulate biomass, LS= litter size, PS = pack
size, and WD = wolf density. The random effect was PackID.

Timeframe	Parameter	β	*SE*	*P*-value	Marginal R^2	Conditional R^2
Annual	Intercept	427.46	29.67	<0.01	0.41	0.87
	HD	-29.51	27.34	0.02		
	TC	-2.43	33.67	0.03		
	UBI	-40.34	32.05	0.51		
	PS	-8.68	25.15	0.05		
	WD	-7.57	18.18	0.28		
Denning	Intercept	238.41	34.43	<0.01	0.35	0.39
	TC	25.44	36.10	0.83		
	UBI	-52.39	36.81	0.07		
	LS	-3.94	26.03	0.04		

Timeframe	Parameter	β	*SE*	*P*-value	Marginal R^2	Conditional R^2
	PS	44.75	26.02	0.01		
Post	Intercept	370.87	33.76	<0.01	0.41	0.60
Denning	TC	35.81	38.76	0.46		
	UBI	-128.73	40.03	0.004		
	PS	46.92	33.03	0.03		
Non-	Intercept	6.09	0.07	<0.01	0.42	0.54
Denning	SD	-123.58	51.61	0.02		
	TC	-44.44	58.71	0.45		
	UBI	24.69	62.34	0.69		
	PS	-7.49	42.65	0.82		
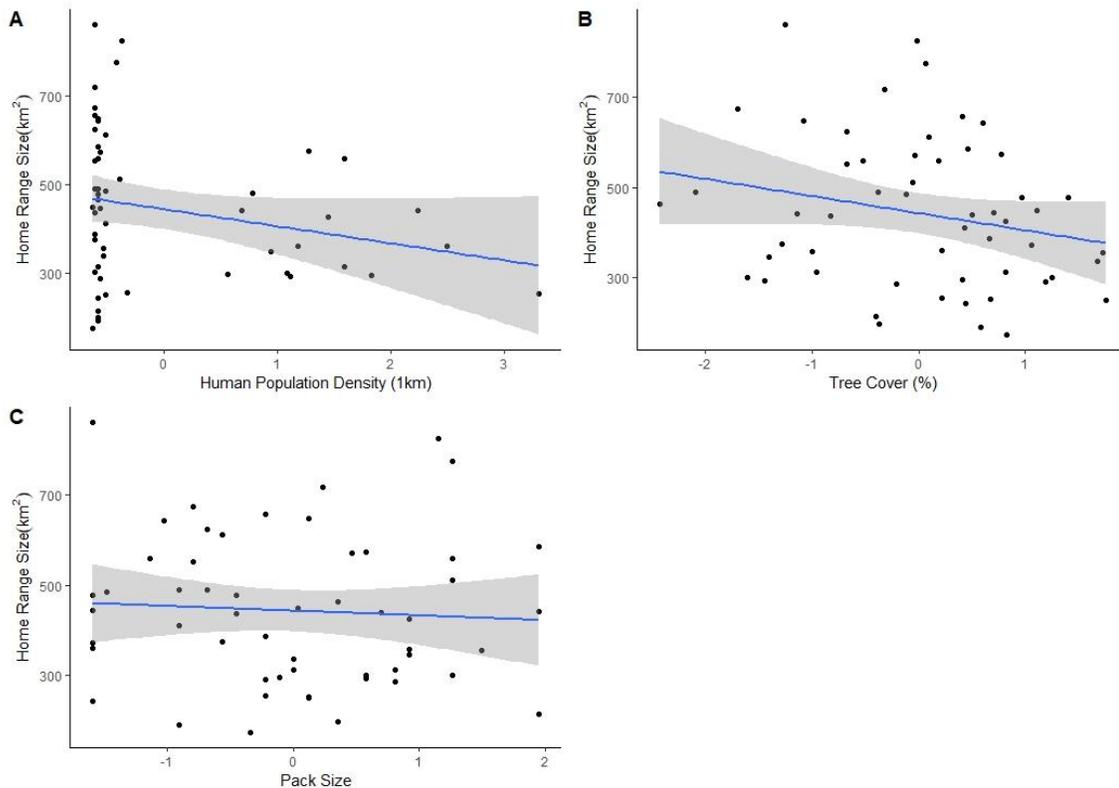
Figure 4. Standardized variables of ecological (human population density (A) and tree cover (B)) and social factors (pack size (C)) influencing annual home range size (km^2) of Mexican wolves between 1 April 2017 and 31 March 2021. The blue line represents the fitted model, the gray shaded region represents the confidence interval for the fitted model, and the black dots represent the raw data.

Litter and pack sizes both influenced home range sizes during the denning season, with larger home ranges correlated with larger packs but smaller litters (Fig. 5, Table 4). Ungulate biomass had a marginal effect on home range size such that wolves exhibited smaller home ranges with higher ungulate biomass (Fig. 5, Table 4). Similar to the annual season, ungulate biomass had the strongest effect on home range size at this timeframe (β=-52.93, Table 4), followed by pack size (β=44.75, Table 4). Tree cover was not

influential in shaping home range size during this season. Altogether, the fixed effects of
the denning model explained 35% of variation in the data while the whole model
explained 39% of the data which results in packs accounting for 4% of variability at the
annual timeframe (Table 4).
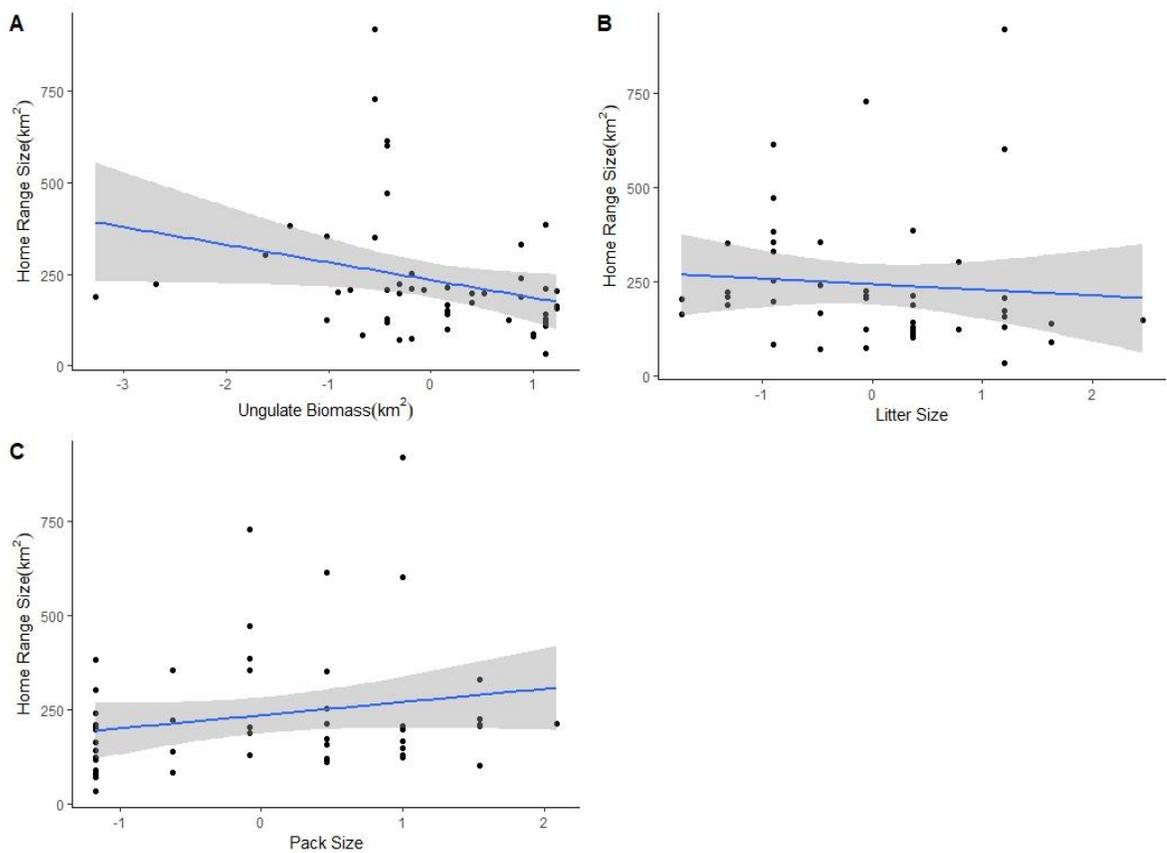
Figure 5. The standardized ecological and social factors (ungulate biomass (A) litter size
(B) and pack size (C)) influencing the denning home range size of Mexican
wolves between 1 April 2017 and 31 March 2021. The blue line represents the
fitted model, the gray shaded region represents the confidence interval for the
fitted model, and the black dots represent the raw data.

Post denning home range size was influenced by ungulate biomass and pack size; and not influenced by tree cover (Table 4). During the post denning period, home range size decreased with increasing ungulate biomass and increased with increasing pack size (Fig. 6). Where both ungulate biomass (β=-128.73, Table 4) and pack size (β=46.92, Table 4) were the strongest variables influencing home range size at the post denning timeframe, respectively. The fixed effects of the post denning model explained 41% of the variation in data while the whole model explained 60%, resulting in packs accounting for 19% of variability at this timeframe (Table 4).
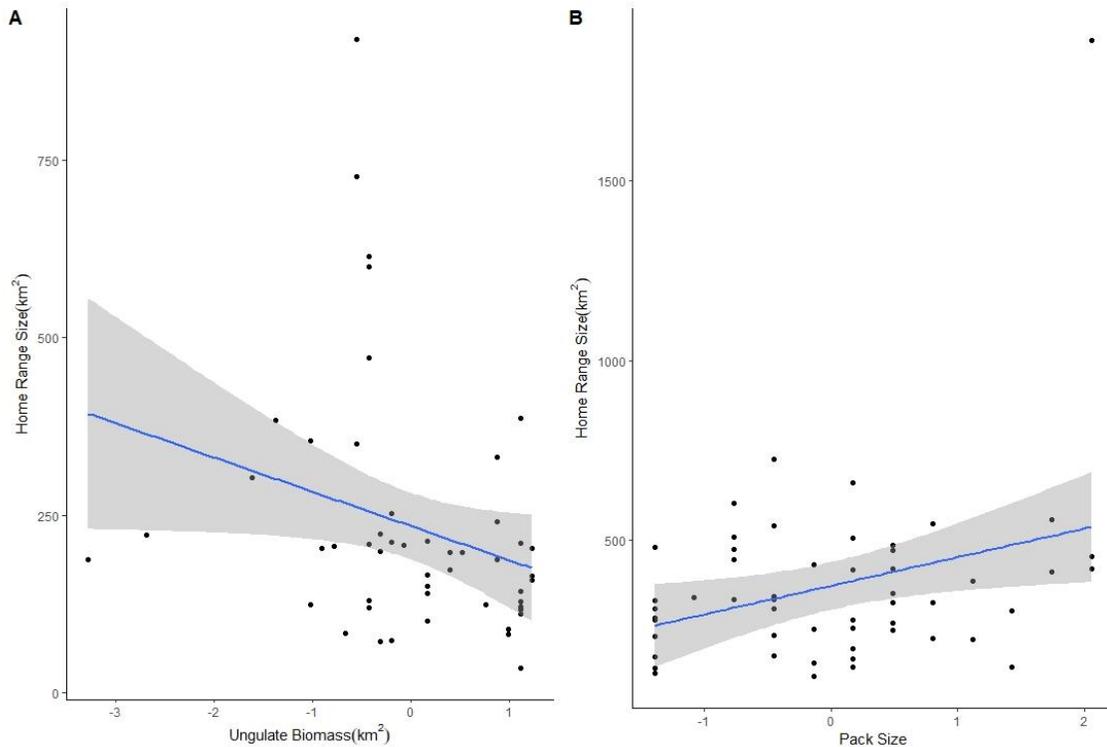
Figure 6. The standardized ecological and social factors (ungulate biomass (A) and pack size (B)) influencing the post denning home range size of Mexican wolves between 1 April 2017 and 31 March 2021. The blue line represents the fitted model, the gray shaded region represents the confidence interval for the fitted model, and the black dots represent the data.

During the non-denning period, snow depth was negatively correlated with home range size (Fig. 7, Table 4) where snow depth also had the strongest effect on the model (β= -123.58, Table 4). Tree cover, ungulate biomass, and pack size were not notably influential during this season. The fixed effects during the non-denning period explained 42% of the data while the whole model explained 54% of the variation in data resulting in packs accounting for 12% of variability at this timeframe (Table 4).
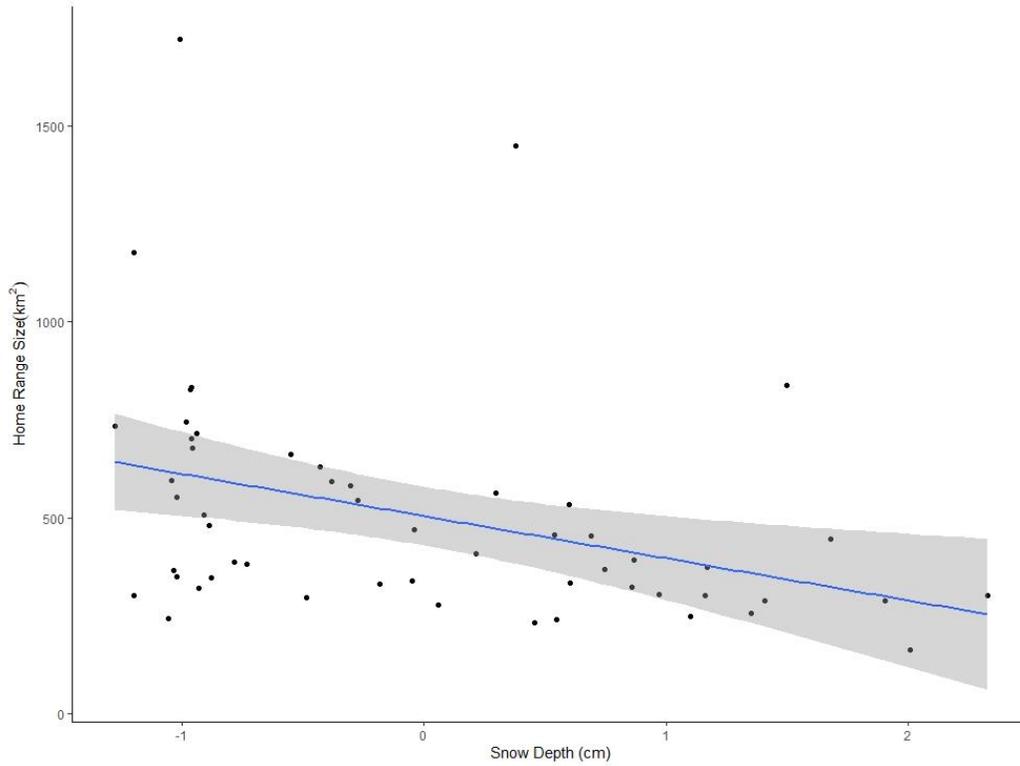
Figure 7. The standardized ecological factor of snow depth (cm) influencing the non-denning home range size of Mexican wolves between 1 April 2017 and 31 March 2021. The blue line represents the fitted model, the gray shaded region represents the confidence interval for the fitted model, and the black dots represent the data.

DISCUSSION

Mexican wolves were reintroduced to the southwest 23 years ago, yet there hasn't been research investigating their ranging patterns and factors influencing home range size until now. I investigated the ecological and social determinants of Mexican wolf home range size over a period of 4 years and 4 timeframes (annual, denning, post denning, non-denning) with GPS collar data from 22 Mexican wolf packs ranging across Arizona and New Mexico. Home range and pack size contracted and expanded between timeframes, ecological variables were similar among timeframes and demonstrated seasonal home range patterns that appeared to mirror seasonal movement of prey. I predicted that both ecological and social variables would influence home range size at all timeframes, and I found that a combination of ecological and social variables shaped Mexican wolf home range size depending on the timeframe.

Home range size varied across timeframes, with average home range sizes ranging from as small as 234 km^2 (smallest 34 km^2) during the denning period, nearly doubling to 443 km^2 over the whole year, and reaching the highest average of 505 km^2 during the non-denning period. The largest recorded home ranges of 1,722 and 1,892 km^2 were observed during the non-denning and post denning periods, respectively. Both these larger home range sizes came from the San Mateo pack in New Mexico where during the post denning season they had a pack size of 13 individuals, and lower than average for prey biomass available in their home range (UBI= 0.73). Similarly, during the non-denning season, the San Mateo pack had 9 individuals and lower than average ungulate

biomass (UBI= 0.74). It could be that due to larger pack size and lower ungulate biomass, this pack had to range farther in search of food, as home range size is often inversely correlated with higher abundance of food (Fisher et al. 2000, Anderson et al. 2005, Loveridge et al. 2009, van Beest et al. 2011, Simchareon et al. 2014, Ward et al. 2018). Additionally, the San Mateo pack didn't share their home range borders with other packs, so they may have had the freedom to range more widely in search of food. The pattern of increasing home range size through the seasons from denning to non-denning is not surprising given that pack movements are restricted when they have dependent pups (denning), with increasing pack mobility (as well as pack size) through the post denning and non-denning periods. Juveniles are known to disperse during the non-denning period (USFWS 2017). The average annual home range may be smaller than the average home range during the non-denning season due to the inclusion of all time periods, including denning and post denning, when pack movements are restricted due to dependent pups, emphasizing the importance of using a multiscale approach to investigating home range patterns.

Pack size also influenced home range size across seasons. During the study period, the average pack size during the denning period was 4 individuals, which increased by 75% in the post denning period to an average of 7 individuals, likely due to surviving pups traveling with the pack, as Mexican wolf pups have a survival rate of about 50% between month of birth (April or May) and September of the same year (USFWS 2017). Pack size decreased by 28% from the post denning to non-denning

period to an average of 5 individuals, likely due to dispersing juveniles and mortalities during this time (USFWS 2017).

Human density is important to include in wolf studies due to conflict, and wolf preference to establish home ranges in areas of low human densities (Mech et al. 1988, Wydeven et al. 2001, Oakleaf et al. 2006). In this study, human density was negatively correlated with home range size at the annual time scale. It is not surprising to find wolves establishing smaller home ranges in areas of higher human density due to wolves avoiding human disturbance and preferring areas of higher tree cover (Mattisson et al. 2013, Kaartinen et al. 2015, Mancinelli et al. 2018). Areas of higher human density also likely represent areas of higher wolf mortality (Oakleaf et al. 2006). Turnbull et al. (2013) reported that from a sample of 100 Mexican wolf mortalities, where cause of death was known, approximately 81% of mortalities were human caused including illegal shootings and vehicle collisions. Thus, the establishment of a home range away from higher areas of human density is critical for wolf survival, reproduction, and habitat use (Oakleaf et al. 2006), and the negative correlation with home range size and human density may be indicative of wolves avoiding human disturbance (Kaartinen et al. 2015). Increased mortality of Mexican wolves in areas of higher human density may prevent establishment of packs in areas of higher human density. However, as the Mexican wolf population increases, smaller annual home ranges in areas of higher human use may promote higher wolf density, increasing competition for prey and space.

The average value of ungulate biomass varied little among the four timeframes, yet negatively impacted home range size of Mexican wolves during the denning

(marginally) and post-denning seasons. The inverse correlation with home range size and prey biomass found in this study is similar to findings reported in other wolf research (Jedrzejewski 2007, Rich et al. 2012) as well as what has been reported for other species. For example, home range size of female elk was inversely correlated with average forage biomass in Alberta and Wisconsin (Anderson et al. 2005); moose home range size in Norway was inversely correlated with forage density; and carnivore population home range sizes were inversely correlated with prey availability in African lions (Loveridge et al. 2009); tigers in Southeast Asia (Simchareon et al. 2014); and coyotes in the Southeast United States (Ward et al. 2018). An inverse correlation with food biomass is typically observed because when resources are abundant individuals or packs don't need to move as much in search of food (Ward et al. 2018). The results herein continue to support the hypothesis that when important resources such as food are abundant, home ranges are smaller (Anderson et al. 2005, Ward et al. 2018). Searching for prey requires important costs per unit of time (Griffiths 1980, Petroelje et al. 2013), and the negative correlation with Mexican wolf home range size likely represents an important energetic balance. During the denning and post denning seasons, wolves travel long distances to bring prey to pups constrained to the den (Mech 1973, Mech et al. 1999) or at rendezvous sites and must travel back and forth repeatedly to feed and maintain pups (Mech 1973). Mexican wolves likely den and set rendezvous sites with access to elk, and the negative correlation with ungulate biomass is likely due to elk being abundant, as the denning season had the highest average of ungulate biomass (UBI = 0.83). Ungulate biomass has been reported as an influential factor to wolf home range size in other studies, where it was concluded

that prey biomass may increase with increasing forest cover (Rich et al. 2012). It could be that forest cover is more influential than prey biomass at the timescales where ungulate biomass was not found influential (annual and non-denning) for annual home range establishment.

High tree cover has been reported as an abiotic factor influencing home range selection of wolf populations at the annual, denning, and post denning timeframes (Trapp et al. 2008, Unger et al. 2009). Specifically, Unger et al. (2009) found higher canopy cover to be significant in gray wolf den site selection, which could be indicative of wolves preferring more vertical protection or a by-product of wolves' selection of tree roots for den sites, which provides more structural integrity and visual obscurity. Similarly, in Poland Theuerkauf et al. (2003) found that wolves selected dry conifer forests for both den and rendezvous sites. Thus, I also hypothesized that tree cover would be influential in the denning and post denning periods for Mexican wolves. In addition to denning and rendezvous sites, tree cover may influence wolf home range selection due to a possible positive correlation with elk abundance and tree cover (Rich et al. 2012), as these higher forested areas are utilized by their preferred prey for diel activity, antipredator responses, and forage availability (Ager et al. 2003, Mao et al. 2005, Roberts et al. 2017, Woodruff et al. 2018). Due to this, wolves may select areas of high tree cover to increase their chances of obtaining prey (Bergman et al. 2006) that they may try to chase into open areas. However, obtaining prey is dependent on first encountering prey. Wolves have been documented to patrol edge areas of open and forested areas, and the hunt may lead elk to forested areas forcing elk to maneuver around obstacles such as

downed trees (Bergman et al. 2006). Wolves may also be handicapped by such obstacles; however, anything that slows down an elk may close the gap in a narrow chase (Bergman et al. 2006), and wolves have been demonstrated to use understory vegetation in forests for stalking prey (Mao et al. 2005). If elk are in areas of higher canopy cover for hiding or escape cover, and wolves may use similar areas for stalking, it may result in wolves selecting the same canopy cover as their prey, possibly explaining the negative correlation with forest cover and annual Mexican wolf home range size. Wolf habitat selection may thus be influenced by prey habitat selection (Mao et al. 2005, Woodruff et al. 2018). Mao et al. (2005) documented that wolf habitat selection paralleled that of elk habitat selection in Yellowstone National Park, and in Ontario, Canada, wolves made disproportionate use of forests in response to high quality moose habitat (Brown 2011). The ecological characteristics of forest cover and elevation in this study of Mexican wolves may also support this hypothesis. Specifically, the average tree cover within seasonal Mexican wolf home ranges increased from the denning through the non-denning season, and elk and deer have been demonstrated to use forested areas of higher canopy cover during spring through the summer likely due to seasonal phenology of preferred forage species (Ager et al. 2003). The relatively high amount of tree cover and ungulate biomass in this study also coincide with a study on livestock depredation risk by Mexican wolves. Amirkhiz et al. (2018) found that livestock depredation risk within the Mexican wolf experimental population area was positively correlated with increasing forest cover and abundance of elk, and these ecological variables were the main variables found to influence ranging patterns by Mexican wolves in this study.

Although tree cover and ungulate biomass were not directly correlated in this data set, possibly due to small sample size or large-scale estimates of ungulate biomass, it is possible that the negative correlation of Mexican wolf home range size with forest cover at the annual scale may demonstrate that Mexican wolves are establishing an annual home range in areas that increase their chances of encountering elk, and thus obtaining elk year-round, and to avoid human disturbance, as previously discussed. Therefore, it is critical to evaluate factors with a multiscale approach as tree cover and ungulate biomass were influential at some timeframes but not others.

Elevation was an ecological variable of interest as it has been positively correlated with home range size in Scandinavian wolves (Mattison et al. 2013), likely due to prey access. Joly et al. (2017) found that wolf den sites in Alaska were selected in areas with elevation low enough to avoid snow but high enough to have access to prey and be close to water. However, elevation in this study area did not vary much across seasons (average range: 2,424-2,490 m), nor did it appear in any of the top models in this study. In this study, elevation was highest during the denning season, which is likely related to elk movement. Similar to the pattern of tree cover, during summer and fall, elk generally spend time in higher elevation areas where forage is available (Brough et al. 2017). As the biological seasons progress to post denning (1 August-31 November) and non-denning (1 December-31 March), the weather is getting progressively cooler and snow falls pushing elk into lower elevation areas, as snow increases energetic costs and can limit access to forage (Messer et al. 2008, Robinson and Merrill 2011, Richard et al. 2014), and predators follow (Alexander et al. 2006, Messer et al. 2008). This may further

support that Mexican wolf seasonal home range selection may mirror that of elk as elevation on average decreased from the denning through the non-denning season, and this pattern is true of seasonal home ranges of elk within the study area in Northeastern Arizona that elk movements decreased from the spring through winter home ranges of elk (Wallace and Krausman 1997).

Previous studies have identified that wolves use roads and snowmobile trails in the winter to alleviate the energetic cost of traveling in snow (Droghini and Boutin 2018b) and have reported a positive correlation between wolf home range and road usage (Mancinelli et al. 2018). If wolves are using roads during the non-denning season to alleviate energetic costs of deeper snow, it may explain the larger home range size during the non-denning period (average 14% larger) as compared to the annual period. Wolves in forested habitats hunt primarily through olfaction (Coulter and Mech 1971) and snowfall may make it harder to detect prey by eliminating scent from the air, in addition to insulating sound and covering tracks (Kyrö et al. 2009). Although wolves are well-adapted to obtaining prey in deep snow (Bergman et al. 2006, Wikenros et al. 2009), encounter rates may be low if wolves have a harder time detecting prey (Vander Vennen et al. 2016), and wolves may need to travel larger distances to find prey. An alternative explanation for the negative correlation between snow depth and home range size is increased hunting success in deeper snow. Several studies have demonstrated that wolf hunting success increases with increasing snow depth (Nelson and Mech 1986, Fuller 1991, Huggard 1993, Wikenros et al. 2009), and less movement with increasing snow depth could be indicative of successful hunts (Droghini and Boutin 2018b). Wolves can

spend 3-5 days at a kill site for large prey such as elk (Metz et al. 2011, Ausband et al. 2016). However, caution should be taken with this interpretation as the snow depth in the Southwest is considerably shallower than those in northern states. Possibly elk in this study area can more simply move to lower elevation to get below the snow line or at least be in more shallow snow, and elk form into large groups at lower elevation in the winter to avoid deep snow, protect calves, and have more access to higher quality forage (Hebblewhite and Pletscher 2002, White et al. 2012). Due to larger groups in the winter, wolves may be able to detect prey better (Hebblewhite and Pletscher 2002); wolf predation on elk has demonstrated to increase with increasing prey group size, where encounter rates and successful kills were higher with elk groups between 6-30 individuals (Hebblewhite and Pletscher 2002), similar to other predators (African wild dogs, Fanshawe and Fitzgibbon 1993; predatory fish, Krause and Godin 1995, Connell 1999). Thus, snow depth may indirectly increase Mexican wolf hunting success by the way it influences elk movements.

Social variables influencing home range size are of particular interest in this study as litter and pack size are critical components of endangered Mexican wolf ecology as a pack living species. Litter size was negatively correlated with Mexican wolf home range size during the denning season, similar to African wild dogs (Pomilia et al. 2015). In preliminary analyses, food caching was not particularly informative on its own; however, packs that are supplementally fed may not have to travel as often or as far to obtain food for the pack and pups, possibly explaining the negative correlation with litter size and denning home range size, warranting further investigation. Alternatively, larger litters

may negatively impact pack movements because packs with large litters need to hunt more often and closer to the den to sustain larger litters as packs must return to the den as soon as possible after hunting (Mech and Boitani 2003). There was large variation in home range size during the denning period. For example, in the 2019 year the Panther Creek pack in Arizona had a litter size of 8 pups and a denning home range size of 34 km^2, while the Sheepherders Baseball Park (SBP) pack during the same year in New Mexico had a litter size of 3, and a home range of 472 km^2. However, litter size likely is not the only variable influencing home range size at this timeframe. The Panther creek pack didn't have any packs around their 95% BBMM border, a pack size of 2, and a 0.92 value for ungulate biomass; compared to the SBP pack which had 3 packs up against their 95% BBMM home range border, a pack size of 4, and a 0.79 value for ungulate biomass. Thus, for the SBP pack even though they had a smaller litter, they may have had to expand their range for food due to lower ungulate biomass, a larger pack, and potential competition from neighboring packs. The potential relationship between litter size, ungulate biomass, and competition for resources warrants further investigation.

The relationships between pack size and home range size were also interesting. Home range size was inversely correlated with pack size at the annual time scale, but positively influenced by pack size during the denning and post-denning seasons. In a seminal paper, Macdonald (1983) demonstrated a positive correlation between wolf pack size and annual home range size, and similar relationships with African lions, spotted hyena (*Crocuta crocuta*), and coyote groups. However more recent publications have not observed this relationship for coyotes (Patterson and Messier 2001) or wolves (Potvin

1988, Mech et al. 1998, Rich et al. 2012, Kittle et al. 2015). Due to the cost of

maintaining a home range including perimeter control, scent marking, and the occasional

intraspecific aggression (Kittle et al. 2015), a home range should be large enough to

encompass pack requirements and small enough to maintain energy efficiency

(Macdonald 1983), which is commonly why there is an inverse relationship between

overall home range and pack size in wolves (Kittle et al. 2015). At the annual scale, the

inverse relationship with home range and pack size held true, however, larger packs may

not always indicate energy efficiency (Schmidt and Mech 1997). The cost of sharing kills

(Packer et al. 1990), some pack members tendency not to contribute to the kill (MacNulty

et al. 2012), and reduced efficiency of group search can outweigh any potential benefits

of larger packs (Fryxell et al. 2007). For example, in Yellowstone National Park, gray

wolf hunting success of elk did not measurably improve beyond pack size of 3 to 4

wolves due to additional pack members withholding effort (MacNulty et al. 2012).

However, Mexican wolves are smaller in stature than their Northern cousins in

Yellowstone National Park but are hunting the same type of elk (rocky mountain elk); it

may be that 5 to 6 Mexican wolves is the optimum pack size for pack efficiency in

hunting, as the beta estimate for pack size was negative during the non-denning season

(average 5 individuals) and annual scale (average 6 individuals). Similarly, results from

other large social carnivores demonstrated more cooperation when hunting larger prey in

larger groups up to a threshold (African lion (Scheel and Packer 1991); African wild dogs

(Creel and Creel 2002)). If a negative correlation represents pack efficiency, then a

positive correlation may be indicative of reduced pack efficiency. Possibly, the positive

correlation between pack size during the denning period suggests that packs have to hunt more often to sustain themselves and their litter, while during the post denning period, with an average of 7 individuals, younger members may not be contributing to the hunt (MacNulty et al. 2012). Thus, Mexican wolf packs during these seasons may be reduced in efficiency. In fact, wolf packs have been known to provision their pups to at least 13 months old (Mech 1995).

The Mexican wolf population has increased yearly over the past 5 years (USFWS 2021). Consequently, I suspected that wolf density would be a social variable influencing annual home range size, but it did not. Mexican wolf packs utilized in this analysis displayed high annual home range overlap (Fig. 2); home range overlap in canids is often exhibited when overlapping packs have related members (Jackson et al. 2017). In fact, intraspecific killings between Mexican wolves are low (USFWS 2017). As of 2017, Mexican wolves in the United States population were on average as related to one another as half-siblings (USFWS 2017), with their population mean relatedness in the United States being 0.25 (USFWS 2017). Alternatively, the amount of overlap seen could be due to relatively high resources (high prey biomass), as seen between wolves and between wolves and coyotes (Petroelje et al. 2021). In addition, lack of effect of wolf density on home range size could be due to the relatively low population of Mexican wolves (186 individuals in Arizona and New Mexico). The average density of Mexican wolves was 0.03 wolves per 100 km^2 in an average of 32,014 km^2 occupied range; as compared to a recent study in Poland found that wolf density of 0.92 wolves per 100 km^2 in a 2,500 km^2 study area where wolf density negatively impacted home range size

(Mysłajek et al. 2018). Any effect of wolf density may be better explained by the number of surrounding packs, as some packs didn't have any surrounding packs (e.g., San Mateo) while others had up to 5 surrounding packs (e.g., SBP; Fig. 2). Mexican wolves may not have yet reached a threshold where density is a limiting factor on establishing an annual home range.

Ecological and social variables influenced home range size at different time scales. The annual home range size of Mexican wolves demonstrated typical annual home range selection as a function of high prey biomass, in addition to low human population densities. Home range size during the denning and post denning periods was largely influenced by social variables (litter and pack sizes) and the ecological variable of ungulate biomass, likely due to increased demand for food to support pups and larger pack sizes, which may reduce pack efficiency. Home range size during the non-denning period was influenced only by snow depth, possibly due to increased energetic costs, or alternatively increased hunting success.

CONCLUSION

Where wolves occur, there is large variation in home range size between and within populations (Fuller et al. 2003, Jedrzejewski et al. 2007, Adams et al. 2008, Mattisson et al. 2013). This was further confirmed in this study and emphasizes the importance of evaluating factors influencing home range size for distinct populations to make data driven decisions for population-specific management. When home range is only studied at the annual time scale, it obscures home range and pack size fluctuations across smaller time periods (seasons) and therefore does not demonstrate what factors are relevant at each scale, which is essential for sensitive species conservation and management.

A lot is known about the general factors influencing home range size of gray wolves, but little is known about the factors influencing Mexican wolf home range size. Some of the relationships found in this study deviate from findings of other wolf research, demonstrating the importance of analyzing spatial ecology of a species with a multiscale approach, including timeframes that may be important to recovering and managing populations. As home range areas during the denning season are significant factors influencing the reproductive success of a wolf pack (Harrington et al. 1983), understanding the factors affecting their denning and post denning ranging behavior may provide critical insight and information to managers as Mexican wolves continue to expand in the MWEPA.

Examining Mexican wolf ranging behavior across multiple spatiotemporal scales has led to a better understanding of how this controversial, highly mobile species navigates through the landscape in space and time in response to ecological and social variables. The information from this research is novel and informative for Mexican wolves. I expect my results will broadly inform management and conservation by promoting data-driven decisions on management actions taken during biological seasons.

LITERATURE CITED

Adams, L. G., R. O. Stephenson, B. W. Dale, R. T. Ahgook, and D. J. Demma. 2008. Population Dynamics and harvest characteristics of wolves in the central Brooks Range, Alaska. Wildlife Monographs 170:1–25.

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

Alexander, S. M., T. B. Logan, and P. C. Paquet. 2006. Spatio-temporal co-occurrence of cougars (*Felis concolor*), wolves (*Canis lupus*) and their prey during winter: A comparison of two analytical methods. Journal of Biogeography 33:2001–2012.

Amirkhiz, R. G., J. K. Frey, J. W. Cain, S. W. Breck, and D. L. Bergman. 2018. Predicting spatial factors associated with cattle depredations by the Mexican wolf (*Canis lupus baileyi*) with recommendations for depredation risk modeling. Biological Conservation 224:327–335.

Anderson, D. P., J. D. Forester, M. G. Turner, J. L. Frair, E. H. Merrill, D. Fortin, J. S. Mao, and M. S. Boyce. 2005. Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. Landscape Ecology 20:257–271.

Asa, C., P. Miller, M. Agnew, J. A. R. Rebolledo, S. L. Lindsey, M. Callahan, and K. Bauman. 2007. Relationship of inbreeding with sperm quality and reproductive success in Mexican gray wolves. Animal Conservation 10:326–331.

Ashenafi, Z. T., T. Coulson, C. Sillero-Zubiri, and N. Leader-Williams. 2005. Behavior and ecology of the Ethiopian wolf (*Canis simensis*) in a human-dominated landscape outside protected areas. Animal Conservation 8:113–121.

Ausband, D. E., M. S. Mitchell, S. B. Bassing, M. Nordhagen, D. W. Smith, and D. R. Stahler. 2016. Dog days of summer: Influences on decision of wolves to move pups. Journal of Mammalogy 97:1282–1287.

Ballard, W. B., J. S. Whitman, C. L. Gardner. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildlife Monographs 98:5-54.

Bates D, M. Mächler, B. Bolker, S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67:1–48. doi: 10.18637/jss.v067.i01.

Bednarz, J. C., 1988. The Mexican wolf: biology, history, and prospects for reestablishment in New Mexico. US Fish and Wildlife Service, Albuquerque, NM.

Benson, J. F., and B. R. Patterson. 2014. Spatial overlap, proximity, and habitat use of individual wolves within the same packs. Wildlife Society Bulletin 39:31–40.

Bergman, E. J., R. A. Garrott, S. Creel, J. J. Borkowski, R. Jaffe, and F. G. Watson. 2006. Assessment of prey vulnerability through analysis of wolf movements and kill sites. Ecological Applications 16:273–284.

Börger, L., N. Franconi, F. Ferretti, F. Meschi, G. D. Michele, A. Gantz, and T. Coulson. 2006. An Integrated Approach to Identify Spatiotemporal and Individual-Level Determinants of Animal Home Range Size. American Naturalist 168:471–485.

Bowen, W. D. 1981. Variation in coyote social organization: the influence of prey size. Canadian Journal of Zoology 59:639–652.

Bradley, E. H., and D. H. Pletscher. 2005. Assessing factors related to wolf depredation of cattle in fenced pastures in Montana and Idaho. Wildlife Society Bulletin 33:1256–1265.

Brough, A. M., R. Justin DeRose, M. M. Conner, and J. N. Long. 2017. Summer-fall home-range fidelity of female elk in northwestern Colorado: Implications for aspen management. Forest Ecology and Management 389:220–227.

Brown, D. E., and H. Shaw. 2002. The Wolf in the Southwest: The Making of an Endangered Species. High-Lonesome Books, Silver City, NM.

Brown, G. S. 2011. Patterns and causes of demographic variation in a harvested moose population: Evidence for the effects of climate and density-dependent drivers. Journal of Animal Ecology 80:1288–1298.

Burnham, K.P. & D.R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edn. Springer-Verlag, Berlin.

Bjorge, R. R., and J. R. Gunson. 1985. Evaluation of wolf control to reduce cattle predation in Alberta. Journal of Range Management 38:483–487.

Calenge, C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Calenge, C. 2015. Home range estimation in R: the adehabitatHR package. The Comprehensive R Archive Network.

https://cran.rproject.org/web/packages/adehabitatHR/adehabitatHR.pdf. Accessed 3 Feb 2021.

Center for International Earth Science Information Network - CIESIN - Columbia University. 2018. Gridded Population of the World, Version 4 (GPWv4): Population Density, Revision 11. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). https://doi.org/10.7927/H49C6VHW. Accessed 11 April 2021.

Ciucci, P., L. Boitani, F. Francisci, and G. Andreoli. 1997. Home range, activity and movements of a wolf pack in central Italy. Journal of Zoology 243:803–819.

Connell, S. D. 2000. Is there safety-in-numbers for prey? Oikos 88:527–532.

Coulter, M. W., and L. D. Mech. 1971. The Wolf: The Ecology and behavior of an endangered species. Journal of Wildlife Management 35:861-864 .

Creel, S. and N. Creel. 2002. The African wild dog. Princeton University Press, Princeton, NJ.

CyVerse Data Commons. 2020. Data Commons. CyVerse Data Commons. <https://datacommons.cyverse.org/browse/iplant/home/shared/commons_repo/curated/MartinezMeyer_et_al_DivDist_2021> Accessed 12 Apr 2021.

Del Solla, S.R., R. Bonduriansky, and R. J. Brooks. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. Journal of Animal Ecology 68:221-234.

Douglas-Hamilton I., T. Krink, and F. Vollrath. 2005. Movements and corridors of African elephants in relation to protected areas. Naturwissenschaften 92:158-163.

Download Mosaic Data Products [DMDP]. 2021. LANDFIRE Program: Data Product
    Mosaic Downloads. <https://landfire.gov/version_download.php#> Accessed 3
    Jul 2021.

Droghini, A., and S. Boutin. 2018a. The calm during the storm: Snowfall events decrease
    the movement rates of grey wolves (*Canis lupus*). PLoS ONE 13:10: e0205742.
    https://doi.org/10.1371/journal.pone.0205742.

Droghini, A., and S. Boutin. 2018b. Snow conditions influence grey wolf (*Canis lupus*)
    travel paths: The effect of human-created linear features. Canadian Journal of
    Zoology 96:39–47.

Fanshawe, J. H., and C. D. Fitzgibbon. 1993. Factors influencing the hunting success of
    an African wild dog pack. Animal Behaviour 45:479–490.

Figueira Machado, R., F. O. Cerezer, C. D. Hendges, and N. C. Cáceres, 2017. Factors
    affecting the home range size of felids (Mammalia, Carnivora) with emphasis on
    three American species. Ecología Austral 27:232-241.

Fisher, D. O. 2000. Effects of vegetation structure, food and shelter on the home range
    and habitat use of an endangered wallaby. Journal of Applied Ecology. 37:660-
    671.

Fletcher, R., and Fortin, M-J. 2019. Spatial Ecology and Conservation Modeling
    Applications with R. Springer International Publishing, Cham, Switzerland.

Fritts, S. H., and L. D. Mech. 1981. Dynamics, movements, and feeding ecology of a
    newly protected wolf population in northwestern Minnesota. Wildlife
    Monographs 80:1-79.

Fryxell, J. M., A. Mosser, A. R. Sinclair, and C. Packer. 2007. Group formation stabilizes predator–prey dynamics. Nature 449:1041–1043.

Fuller, T. K., L. D. Mech, and J. F. Cochran. 2010. Wolf population dynamics. In: Mech, L. D., and L. Boitani (Eds.), Wolves: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago, Illinois, pp. 161–191.

Gosling, L. M., W. J. Sutherland, R. Woodroffe, and J. Ginsberg. 2000. Ranging behaviour and vulnerability to extinction in carnivores. Pages 125–140 *in*. Behaviour and Conservation Series. Cambridge University Press, Cambridge, U.K.

Griffiths, D. 1980. Foraging costs and relative prey size. The American Naturalist 116:743–752.

Gros, P. M., M. J. Kelly, and T. M. Caro. 1996. Estimating carnivore densities for conservation purposes: Indirect methods compared to baseline demographic data. Oikos 77:197-206

Gurarie, E., J. Suutarinen, I. Kojola, and O. Ovaskainen. 2011. Summer movements, predation and habitat use of wolves in human modified boreal forests. Oecologia 165:891–903.

Harrington, F. H., L. David Mech, and S. H. Fritts. 1983. Pack size and Wolf Pup Survival: Their relationship under varying ecological conditions. Behavioral Ecology and Sociobiology 13:19–26.

Harrison, X. A., L. Donaldson, M. E. Correa-Cano, J. Evans, D. N. Fisher, C. Goodwin, B. Robinson, D. J. Hodgson, and R. Inger. 2018. A brief introduction to mixed

effects modelling and multi-model inference in ecology. PeerJ 6: e4794. doi: 10.7717/peerj.4794.

Hayes R. D., and A. S. Harestad. 2000. Demography of recovering wolf population in the Yukon. Canadian Journal of Zoology 78:36-48.

Hayne, D.W. 1949. Calculation of Size of Home Range. Journal of Mammalogy 30:1-18.

Hebblewhite, M., and D. H. Pletscher. 2002. Effects of elk group size on predation by wolves. Canadian Journal of Zoology 80:800–809.

Herfindal, I., J. D. C. Linnell, J. Odden, E. B. Nilsen, and R. Andersen. 2005. Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). Journal of Zoology 265:63–71.

Hesselbarth, M. H. K., M. Sciaini, K.A. With, K. Wiegand, and J. Nowosad. 2019. landscapemetrics: an open-source R tool to calculate landscape metrics. Ecography 42:1648-1657.

Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using Brownian bridges. Ecology 88:2354–2363.

Houle, M., D. Fortin, C. Dussault, R. Courtois, and J.-P. Ouellet. 2010. Cumulative effects of forestry on habitat use by gray wolf (*Canis lupus*) in the boreal forest. Landscape Ecology 25:419–433.

Huggard, D. J. 1993. Effect of snow depth on predation and scavenging by gray wolves. The Journal of Wildlife Management 57:382–388.

Jackson, C. R., R. J. Groom, N. R. Jordan, and J. W. McNutt. 2017. The effect of relatedness and pack size on territory overlap in African wild dogs. Movement Ecology 5. Doi https://doi.org/10.1186/s40462-017-0099-8.

Jedrzejewski, W., K. Schmidt, J, Theuerkauf, B, Jedrzejewska, and R, Kowalczyk. 2007. Territory size of wolves *Canis lupus*: linking local (Bialowieza Primeval Forest, Poland) and Holarctic-scale patterns. Ecography 30:66-76.

Joly, K., M. S. Sorum, and M. D. Cameron. 2018. Denning Ecology of Wolves in East-Central Alaska, 1993–2017. Arctic 71:444–455.

Kaartinen, S., H. Antikainen, and I. Kojola. 2015. Habitat model for a Recolonizing Wolf (*Canis lupus*) population in Finland. Annales Zoologici Fennici 52:77–89.

Kie, J. G. 2013. A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. Animal Biotelemetry 1:1-13.

Kittle, A. M., M. Anderson, T. Avgar, J. A. Baker, G. S. Brown, J. Hagens, E. Iwachewski, S. Moffatt, A. Mosser, B. R. Patterson, D. E. B. Reid, A. R. Rodgers, J. Shuter, G. M. Street, I. D. Thompson, L. M. Vander Vennen, and J. M. Fryxell. 2015. Wolves adapt territory size, not pack size to local habitat quality. Journal of Animal Ecology 84:1177–1186.

Koehler, G. M., and M. G. Hornocker. 1989. Influences of Seasons on Bobcats in Idaho. Journal of Wildlife Management 53:197–202.

Krause, J., and J.-G. J. Godin. 1995. Predator preferences for attacking particular prey group sizes: Consequences for predator hunting success and prey predation risk. Animal Behaviour 50:465–473.

Kunkel, K., and D. H. Pletscher. 2001. Winter Hunting Patterns of Wolves in and Near Glacier National Park, Montana. Journal of Wildlife Management 65:520–530.

Kyrö E. M., T. Grönholm, H. Vuollekoski, A. Virkkula, M. Kulmala, and L. Laakso. 2009. Snow scavenging of ultrafine particles: field measurements and parameterization. Boreal Environmental Research 14:527–538.

Loveridge, A. J., M. Valeix, Z. Davidson, F. Murindagomo, H. Fritz, and D. W. Macdonald. 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. Ecography 32:953–962.

Luke, S. G. 2017. Evaluating significance in linear mixed-effects models in R. Behavior Research Methods 49:1494–1502.

Macdonald, D. W. 1983. The ecology of carnivore social behaviour. Nature 301:379–384.

MacNulty, D. R., D. W. Smith, L. D. Mech, J. A. Vucetich, and C. Packer. 2012. Nonlinear effects of group size on the success of Wolves Hunting Elk. Behavioral Ecology 23:75–82.

Main, M. T., R. A. Davis, D. Blake, H. Mills, and T. S. Doherty. 2020. Human impact overrides bioclimatic drivers of red fox home range size globally. Diversity and Distributions 26:1083-1092.

Mancinelli, S., L. Boitani, and P. Ciucci. 2018. Determinants of home range size and space use patterns in a protected wolf (*Canis lupus*) population in the central Apennines, Italy. Canadian Journal of Zoology 96:828–838.

Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H.
Merrill. 2005. Habitat selection by Elk before and after Wolf reintroduction in
Yellowstone National park. Journal of Wildlife Management 69:1691–1707.

Martínez-Meyer, E., A. González-Bernal, J. A. Velasco, T. L. Swetnam, Z. Y. González-
Saucedo, J. Servín, C. A. López-González, J. K. Oakleaf, S. Liley, and J. R.
Heffelfinger. 2021. Rangewide habitat suitability analysis for the Mexican wolf
(*Canis lupus baileyi*) to identify recovery areas in its historical distribution.
Diversity and Distributions 27:642–654.

Mattisson, J., H. Sand, P. Wabakken, V. Gervasi, O. Liberg, J. D. C. Linnell, G. R.
Rauset, and H. C. Pedersen. 2013. Home range size variation in a recovering wolf
population: evaluating the effect of environmental, demographic, and social
factors. Oecologia 173:813–825.

McBride, R. T., 1980. The Mexican Wolf (*Canis lupus baileyi*): a historical review and
observations on its status and distribution: a progress report to the US fish and
wildlife service. US Fish and Wildlife Service, Albuquerque, NM.

Mech. 1995. Summer movements and behavior of an arctic wolf, *Canis lupus*, pack
without pups. Canadian Field Naturalist. 109(4): 473-75.

Mech, L. D. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis.

Mech, L.D., S. H. Fritts, G. L. Radde, W. J. Paul. 1988. Wolf distribution and road
density in Minnesota. Wildlife Society Bulletin. 16:85–87.

Mech, D. L. 1973. Wolf numbers in the Superior National Forest of Minnesota. Research Paper NC-97. St. Paul, MN: U.S. Dept. of Agriculture, Forest Service, North Central Forest Experiment Station.

Mech, L.D., L. G. Adams, T. J. Meier, J. W. Burch, B. W. Dale. 1998. The Wolves of Denali. University of Minnesota Press, Minneapolis, Minnesota, USA.

Mech, L. D., P. C. Wolf, and J. M. Packard. 1999. Regurgitative food transfer among wild wolves. Canadian Journal of Zoology 77:1192–1195.

Mech, L. D., and L. Boitani. 2003. Wolves: Behaviour, Ecology, and Conservation. University of Chicago Press, Chicago, IL.

Messer, M. A., R. A. Garrott, S. Cherry, P. J. White, F. G. R. Watson, and E. Meredith. 2008. The Ecology of Large Mammals in Central Yellowstone - Sixteen Years of Integrated Field Studies. Academic Press.

Metz, M. C., J. A. Vucetich, D. W. Smith, D. R. Stahler, and R. O. Peterson. 2011. Effect of sociality and season on gray wolf (*Canis lupus)* foraging behavior: Implications for estimating summer kill rate. PLoS ONE 6(3): e17332.https://doi.org/10.1371/journal.pone.0017332.

Miller, T. A., R. P. Brooks, M. J. Lanzone, J. Cooper, K. O'Malley, D. Brandes, A. Duerr, and T. E. Katzner. 2017. Summer and winter space use and home range characteristics of Golden Eagles (*Aquila chrysaetos*) in eastern North America. Condor 119:697–719.

Mohr, C.O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223-249.

Morehouse, A. T., and M. S. Boyce. 2017. Troublemaking carnivores: conflicts with humans in a diverse assemblage of large carnivores. Ecology and Society 22:3-15.

Mysłajek, R. W., M. Tracz, M. Tracz, P. Tomczak, M. Szewczyk, N. Niedźwiecka, and S. Nowak. 2018. Spatial organization in wolves *Canis lupus* recolonizing north-west Poland: Large territories at low population density. Mammalian Biology 92:37–44.

Naidoo, R., P. Du Preez, G. Stuart-Hill, L. C. Weaver, M. Jago, and M. Wegmann. 2012. Factors affecting intraspecific variation in home range size of a large African herbivore. Landscape Ecology 27:1523-1534.

Nakagawa S, H., and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences 105:19052–19059.

National Snow and Ice Data Center [NSIDC]. 2003. | National Snow and Ice Data Center. <https://nsidc.org/data/g02158> Accessed 3 June 2021.

Nelson, M. E., and L. D. Mech. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. Journal of Wildlife Management 50:471–474.

Noonan, M. J., M. A. Tucker, C. H. Fleming, T. S. Akre, S. C. Alberts, A. H. Ali, J. Altmann, P. C. Antunes, J. L. Belant, D. Beyer, and N. Blaum. 2018. A comprehensive analysis of autocorrelation and bias in home range

estimation. Ecological Monographs 89(2). e01344. doi:

https://doi.org/10.1002/ecm.1344.

Oakleaf, J. K., C. Mack, and D. L. Murray. 2003. Effects of wolves on livestock calf
survival and movements in Central Idaho. Journal of Wildlife Management
67:299–306.

Oakleaf, J. K., D. L. Murray, J. R. Oakleaf, E. E. Bangs, C. M. Mack, D. W. Smith, J. A.
Fontaine, M. D. Jimenez, T. J. Meier, and C. C. Niemeyer. 2006. Habitat selection
by recolonizing wolves in the northern Rocky Mountains of the United States.
Journal of Wildlife Management 70:554–563.

Okarma, H., W. Jędrzejewski, K. Schmidt, S. Śnieżko, A. N. Bunevich, B. Jędrzejewska,
W. Jedrzejewski, S. Sniezko, and B. Jedrzejewska. 1998. Home Ranges of
Wolves in Białowieża Primeval Forest, Poland, Compared with Other Eurasian
Populations. Journal of Mammalogy 79:842-852.

Packer, C., D. Scheel, and A. E. Pusey. 1990. Why Lions form groups: Food Is Not
Enough. American Naturalist 136:1–19.

Patterson, B. R., and F. Messier. 2001. Social Organization and space use of Coyotes in
eastern Canada relative to prey distribution and abundance. Journal of
Mammalogy 82:463–477.

Petroelje, T. R., J. L. Belant, D. E. Beyer, G. Wang, and B. D. Leopold. 2013.
Population-level response of Coyotes to a pulsed resource event. Population
Ecology 56:349–358.

Petroelje, T. R., T. M. Kautz, D. E. Beyer, and J. L. Belant. 2021. Interference competition between wolves and coyotes during variable prey abundance. Ecology and Evolution 11:1413–1431.

Pomilia, M. A., J. W. Mcnutt, and N. R. Jordan. 2015. Ecological predictors of African wild dog ranging patterns in northern Botswana. Journal of Mammalogy 96:1214–1223.

Potvin, F. 1988. Wolf movements and population dynamics in Papineau-Labelle Reserve, Quebec. Canadian Journal of Zoology 66:1266–1273.

Powell, R. A., and M. S. Mitchell. 2012. What is a home range? Journal of Mammalogy 93:948-958.

Reed, J. E., W. B. Ballard, P. S. Gipson, B. T. Kelly, P. R. Krausman, M. C. Wallace, and D. B. Wester. 2006. Diets of Free-Ranging Mexican Gray Wolves in Arizona and New Mexico. Wildlife Society Bulletin 34:1127–1133.

Richard, J. H., J. Wilmshurst, and S. D. Côté. 2014. The effect of snow on space use of an alpine ungulate: Recently fallen snow tells more than cumulative snow depth. Canadian Journal of Zoology 92:1067–1074.

Rich, L. N., M. S. Mitchell, J. A. Gude, and C. A. Sime. 2012. Anthropogenic mortality, intraspecific competition, and prey availability influence territory sizes of wolves in Montana. Journal of Mammalogy 93:722–731.

Rivrud, I. M., L. E. Loe, and A. Mysterud, A. 2010. How does local weather predict red deer home range size at different temporal scales? Journal of Animal Ecology 79:1280-1295.

Roberts, C. P., J. W. Cain III, and R. D. Cox. 2017. Identifying ecologically relevant scales of habitat selection: Diel Habitat selection in Elk. Ecosphere 8:1–16.

Robinson, B. G., and E. H. Merrill. 2011. The influence of snow on the functional response of grazing ungulates. Oikos 121:28–34.

Scheel, D., and C. Packer. 1991. Group hunting behaviour of Lions: A search for cooperation. Animal Behaviour 41:697–709.

Schmidt, P. A., and L. D. Mech. 1997. Wolf Pack size and food acquisition. American Naturalist 150:513–517.

Simchareon, A., T. Savini, G. A. Gale, S. Simcharoen, S. Duangchantrasiri, S. Pakpien, and J. L. D. Smith. 2014. Female tiger *Panthera tigris* home range size and prey abundance: important metrics for management. Oryx 48:370–377.

Smith, D. W., T. D. Drummer, K. M. Murphy, D. S. Guernsey, and S. B. Evans. 2004. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. Journal of Wildlife Management 68:153–166.

Theuerkauf, J., W. Jedrzejewski, K. Schmidt, and R. Gula. 2003. Spatiotemporal segregation of wolves from humans in the Bialowieza Forest (Poland). The Journal of Wildlife Management 67:706–716.

Trapp, J. R., P. Beier, C. Mack, D. R. Parsons, and P. C. Paquet. 2008. Wolf, *Canis lupus*, den site selection in the Rocky Mountains. Canadian Field-Naturalist 122:49–56.

Treves, A., and J. Bruskotter. 2014. Tolerance for predatory wildlife. Science 344:476–477.

Turnbull, T. T., J. W. Cain III, and G. W. Roemer. 2013. Anthropogenic impacts to the recovery of the Mexican Gray Wolf with a focus on trapping-related incidents. Wildlife Society Bulletin 37:311–318.

Unger, D. E., P. W. Keenlance, B. E. Kohn, and E. M. Anderson. 2009. Factors influencing homesite selection by gray wolves in Northwestern Wisconsin and East-central Minnesota. Recovery of Gray Wolves in the Great Lakes Region of the United States. Springer, New York.

U.S. Fish and Wildlife Services [USFWS]. 2015. Endangered and Threatened Wildlife and Plants; Revision to the Regulations for the Nonessential Experimental Population of the Mexican wolf. Retrieved from: https://www.fws.gov/southwest/es/ Accessed 13 Oct 2021.

United States Fish and Wildlife Service [USFWS]. 2017. Mexican Wolf Biological Report: Version 2. Region 2, Albuquerque, New Mexico, USA.

United States Fish and Wildlife Service [USFWS]. 2018. Mexican Wolf Recovery Program: Progress Report #20. Mexican Wolf Recovery Documents. <https://www.fws.gov/southwest/es/mexicanwolf/recoverydocuments.html> Accessed 3 Sep 2021.

U.S. Fish and Wildlife Service [USFWS]. 2019. Mexican Wolf Recovery Program: Progress Report #21. Mexican Wolf Recovery Documents. <https://www.fws.gov/southwest/es/mexicanwolf/recoverydocuments.html> Accessed 3 Sep 2021.

U.S. Fish and Wildlife Service [USFWS]. 2021. Mexican Wolf. Southwest Region

    Ecological Services.

    <https://www.fws.gov/southwest/es/mexicanwolf/#:~:text=A%20Mexican%20wo

    lf%20in%20the,Credit%3A%20Mexican%20Wolf%20IFT.&text=The%20recent

    %20Mexican%20wolf%20count%20indicates%20that%20the%20population%20

    of,a%20minimum%20of%20131%20animal>. Accessed 1 April 2021.

van Beest, F. M., I. M. Rivrud, L. E. Loe, J. M. Milner, and A. Mysterud. 2011. What

    determines variation in home range size across spatiotemporal scales in a large

    browsing herbivore? Journal of Animal Ecology 80:771–785.

Vander Vennen, L. M., B. R. Patterson, A. R. Rodgers, S. Moffatt, M. L. Anderson, and

    J. M. Fryxell. 2016. Diel movement patterns Influence daily variation in wolf kill

    rates on moose. Functional Ecology 30:1568–1573.

Wallace, M. C., and P. R. Krausman. 1997. Movements and home-ranges of elk in

    eastern Arizona. In Proceedings of the 1997 deer and elk workshop. Rio Rico,

    Arizona. Arizona Department of Game and Fish, Phoenix (pp. 184-185).

Walter, W.D., D. P. Onorato, and J. W. Fischer. 2015. Is there a single best estimator?

    Selection of home range estimators using area-under-the-curve. Movement

    Ecology 3:1-11.

Ward, J. N., J. W. Hinton, K. L. Johannsen, M. L. Karlin, K. V. Miller, and M. J.

    Chamberlain. 2018. Home range size, vegetation density, and season influences

    prey use by coyotes (*Canis latrans*). PloS ONE 13. Doi:

    https://doi.org/10.1371/journal.pone.0203703.

White, P. J., K. M. Proffitt, and T. O. Lemke. 2012. Changes in Elk Distribution and group sizes after Wolf Restoration. The American Midland Naturalist 167:174–187.

Wikenros, C., H. Sand, P. Wabakken, O. Liberg, and H. C. Pedersen. 2009. Wolf predation on moose and roe deer: Chase distances and outcome of encounters. Acta Theriologica 54:207–218.

Woodroffe, R. 2011. Ranging behaviour of African wild dog packs in a human dominated landscape. Journal of Zoology. 283:88–97.

Woodroffe, R., S. Thirgood and A. Rabinowitz. (Eds.). 2005. People and wildlife, conflict or co-existence? Cambridge University Press.

Woodruff, S. P., M. D. Jimenez, and T. R. Johnson. 2018. Characteristics of winter wolf kill sites in the southern Yellowstone Ecosystem. Journal of Fish and Wildlife Management 9:155–167.

Worton, B.J., 1989. Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. Ecology 70:164-168.

Wydeven, A.P., D. J. Mladenoff, T. A. Sickley, B. E. Kohn, J. L. Hansen. 2001. Road density as a factor in habitat selection by wolves and other carnivores in the Great Lakes Region. Endangered Species Update 18:110–114.

Wydeven A. P., R. N. Schultz, and R. P. Thiel. 1995. Monitoring of a gray wolf (*Canis lupus*) population in Wisconsin, 1979-1991. In: Carbyn L. H., S .H. Fritts, D. R. Seip (Eds). Ecology and conservation of wolves in a changing world, Canadian Circumpolar Institute, Edmonton, Alberta, pp 147-156.

Zuur, A. F., and E. N. Ieno. 2016. A protocol for conducting and presenting results of regression-type analyses. Methods in Ecology and Evolution 7:636–645.

Zuur A, E. N. Ieno, N. J. Walker, A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer Sciences and Business Media, New York.

APPENDIX

Appendix A: Home range sizes (km^2) as estimated using Brownian Bridge Movement Model (BBMM) 95% UD for each individual wolves from 22 Mexican wolf packs, per timeframe in the Mexican Wolf Experimental Population Areas (MWEPA) Zone 1, United States. F=female; M= male.

Pack	Primary Year	Wolf ID/Sex	Annual (km^2)	Denning (km^2)	Post Denning (km^2)	Non-Denning (km^2)	Total GPS Locations
Bear Wallow	2017	1335/F	300.95	196.79	227.18	324.04	1,001
Hoodoo	2017	1333/F	313.28	213.04	351.89	289.56	800
	2018	1333/F	359.43	166.13	327.52	369.57	783
	2019	1333/F	347.09	207.51	325.75	305.66	937
	2020	1333/F	441.46	149.20	302.76	534.78	906
Lava	2017	1405/F	859.43	383.50	478.92	1177.99	600
	2018	1405/F	488.62	303.10	474.36	301.91	649
	2019	1405/F	673.15	222.11	445.69	734.56	700
	2020	1405/F	463.72	187.76	504.94	366.33	770
Leopold	2017	1346/F	410.43	120.91	341.46	445.89	1,410
	2018	1346/F	444.48	203.51	332.96	453.00	1,413
	2019	1346/F	373.66	82.00	233.12	380.87	1,351
	2020	1346/F	476.93	210.63	278.49	469.25	1,289
Luna	2017	1158/M	488.41	354.12	336.23	595.16	330
	2018	1158/M	717.28	664.92	660.14	833.97	223
	2019	1158/M	655.83	614.60	539.63	479.57	250

Pack	Primary Year	Wolf ID/Sex	Annual (km^2)	Denning (km^2)	Post Denning (km^2)	Non-Denning (km^2)	Total GPS Locations
Mangas	2017	1296/M	571.93	72.20	420.38	746.05	650
	2018	1296/M	611.17	202.70	725.54	552.63	648
	2019	1296/M	558.36	129.47	472.56	700.85	658
	2020	1296/M	584.05	206.24	557.01	629.92	637
Panther	2017	1339/F	641.76	386.48	284.83	1450.96	700
Creek	2019	1683/F	447.83	34.43	276.71	564.24	651
	2020	1683/F	313.39	331.14	235.67	301.10	767
Prieto	2017	1251/F	337.64	208.75	342.53	347.46	1,372
	2018	1251/F	355.59	223.71	387.39	319.19	1,350
	2019	1251/F	250.2	124.27	198.84	242.46	1,346
Sheepherders	2017	1553/F	374.56	252.83	335.69	387.08	619
Baseball	2018	1553/F	552.65	198.35	335.61	714.47	629
Park	2019	1553/F	623.29	472.22	509.59	677.01	639
	2020	1553/F	648.06	727.38	421.28	662.86	641
Elk Horn	2018	1294/F	439.43	124.12	418.54	543.70	725
	2019	1294/F	425.11	402.14	411.46	337.98	730
	2020	1294/F	296.48	140.15	251.70	330.24	726
Frieborn	2018	1443/F	292.43	173.16	223.29	348.44	686
	2020	1443/F	478.19	83.54	431.03	507.08	631
Iron Creek	2018	1278/F	287.39	110.51	248.31	372.98	650
	2019	1278/F	119.16	187.62	169.96	231.99	705
	2020	1278/F	213.81	128.32	145.54	248.82	654

Pack	Primary Year	Wolf ID/Sex	Annual (km^2)	Denning (km^2)	Post Denning (km^2)	Non-Denning (km^2)	Total GPS Locations
Pine Spring	2018	1394/M	254.57	72.87	158.80	334.29	912
Prime	2018	1471/M	253.19	142.59	146.20	276.81	280
Canyon	2019	1471/M	574.27	158.02	486.98	593.51	239
Saffel	2018	1441/M	300.16	211.44	254.55	257.38	671
	2019	1567/F	293.09	100.91	269.60	301.74	700
San Mateo	2018	1399/F	823.71	119.98	544.77	1,722.18	669
	2019	1399/F	774.15	600.72	454.27	827.21	642
	2020	1399/F	511.75	919.74	1,892.20	582.04	632
Sierra Blanca	2018	1550/F	359.45	207.84	309.20	456.86	651
	2020	1550/F	558.37	375.14	602.34	391.42	871
Colibri	2019	1555/M	483.69	163.63	175.47	838.39	1,553
Rocky	2019	1489/F	386.34	240.37	130.74	409.81	715
Prairie	2020	1489/F	174.91	88.72	120.92	240.97	805
Castle Rock	2020	1686/F	191.29	117.21	176.88	162.15	959
Eagle Creek	2020	1477/M	244.07	197.55	144.75	288.88	1,446
Pitchfork Canyon	2020	1853/F	436.07	350.63	310.11	295.86	1,851