Received: 24 February 2022 | Revised: 28 October 2022 | Accepted: 30 October 2022

DOI: 10.1002/wsb.1416

RESEARCH ARTICLE

WILDLIFE SOCIETY BULLETIN

Camera trapping as a method for estimating abundance of Mexican wolves

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Funding information

Endangered Species Act Section 6; Federal Aid in Wildlife Restoration Act; U.S. Fish and Wildlife Service; Heritage Fund IIAPM

Abstract

Estimating wildlife abundance, particularly for rare and elusive species, is challenging because of time, cost, and methodological constraints. The Mexican wolf (*Canis lupus baileyi*), a federally-listed endangered subspecies of gray wolf, is currently monitored using ground and aerial methods to obtain a minimum known population count. As the Mexican wolf population has grown and expanded, the time and cost required to monitor the subspecies has increased. We investigated the efficacy of camera trapping for estimating Mexican wolf abundance by comparing the accuracy, precision, and cost of camera trapping to those obtained with current monitoring techniques. Between 1 November 2019 and 31 July 2020, we collected 13,317 photos of wolves from 124 camera traps in Arizona where Mexican wolves were known to occur, excluding tribal lands. We used a spatial mark-resight analysis to estimate abundance for both winter (November 2019 through February 2020) and summer (April through July 2020) seasons, with and without the assistance of global positioning system (GPS) telemetry data to identify individual wolves. Combined with GPS data, camera trapping provided a summer abundance estimate ($\hat{N}$ = 50, 95% CI = 37–64) that was 14% lower than the 2019 minimum known population count (*N* = 59), but included the minimum known population count in the 95% confidence interval.

The summer no telemetry abundance estimate was 27% below the minimum known population count ($\hat{N}$ = 43, 95% CI = 30–56). During winter, abundance estimates obtained from camera trapping (no telemetry: $\hat{N}$ = 33, 95% CI = 15–52; telemetry: $\hat{N}$ = 45, 95% CI = 28–62), were much lower than the 2019 Mexican wolf minimum known population count (winter: N = 62), but included the minimum known population count in the 95% confidence interval for the winter telemetry dataset. A cost comparison indicated that the first-year camera trapping equipment expenses were 1.7 times the equipment cost of the current method and that camera trapping equipment expenses in subsequent years were equivalent to the equipment cost of the current method, and required at least 1.4 times the labor hours. We provide recommendations to potentially improve Mexican wolf abundance estimates and minimize camera trapping expenses. The results of our project may help managers make appropriate decisions for their population monitoring needs, while considering budget, staffing capabilities, precision, and accuracy.

KEYWORDS

abundance, Arizona, camera trap, *Canis lupus baileyi*, Mexican wolf, spatial mark-resight

Obtaining accurate estimates of abundance is fundamental for supporting credible management and conservation actions (Williams et al. 2002, Fryxell et al. 2014). Abundance estimates are used to monitor population levels, set hunting and fishing harvest limits, and inform the listing or delisting of threatened and endangered species under the Endangered Species Act (Williams et al. 2002, Alisauskas et al. 2011, Kahn et al. 2019). While abundance estimates are helpful for wildlife management and conservation, obtaining reliable estimates can be logistically challenging due to time and budget constraints, or the biological characteristics of a species (Witmer 2005, Takashina et al. 2018). It can be particularly difficult to estimate abundance of species that are elusive, sparse, or wide-ranging (Gerber et al. 2014, Murphy et al. 2019).

The Mexican wolf (*Canis lupus baileyi*) is the most distinct subspecies of gray wolf in North America (Bogan and Melhop 1983, García-Moreno et al. 1996, vonHoldt et al. 2011). In 2015, the United States Fish and Wildlife Service (USFWS) amended the status of the Mexican wolf by listing it separately as an endangered subspecies (USFWS 2015*a*). Although Mexican wolves were extirpated from Arizona and New Mexico in the mid-1900s, captive-bred Mexican wolves were reintroduced into the Blue Range Wolf Recovery Area in eastern Arizona starting in 1998 (USFWS 2017*a*). The population has steadily grown in the last decade and the 2021 year-end minimum known population count of Mexican wolves in the Mexican Wolf Experimental Population Area (MWEPA) in Arizona and New Mexico was 196 individuals (USFWS 2022). The recovery criteria for delisting Mexican wolves in the United States requires the population to average at least 320 individuals for 8 years, with the final 3 years exceeding 320 individuals (USFWS 2017*a*).

The existing method for monitoring the Mexican wolf population is to maintain at least one collared individual in each pack, which allows managers to conduct annual ground and aerial counts to enumerate the minimum number of individuals in each pack (hereafter, Interagency Field Team [IFT] method; USFWS 2017*b*). The total number of Mexican wolves observed by the IFT method is considered a minimum known population count (hereafter, IFT count). The Mexican wolf IFT counted 44 Mexican wolf packs in the MWEPA at the end of 2021, with a pack defined as 2 or more individuals (USFWS 2022). The IFT method presents various challenges, because; 1) the counts are time intensive and costly; 2) costs for collaring at least one individual in every pack will continue to rise if the number of packs continue to increase; and 3) it does not account for imperfect detection of animals within packs or lone animals, so that the estimate is biased low if detection is <1. To address these challenges, managers desire an alternative method for monitoring Mexican wolf abundance.

Analysis of camera trapping data with spatial mark-resight methods is an established abundance estimation method previously used on other elusive species (Murphy et al. 2019, Sharma et al. 2021). Camera trapping techniques have the benefit of reducing risks and disturbance associated with handling wildlife while also potentially reducing the cost and labor required for long-term monitoring of rare and wide-ranging species (Rovero and Marshall 2009, Welbourne et al. 2015, Jacobs and Ausband 2018). Abundance estimation with camera trapping has primarily been applied to naturally marked species and analyzed in a mark-recapture framework (Trolle and Kéry 2003, Silver et al. 2004, Marnewick et al. 2008). Mexican wolves typically lack distinctive natural marks, but because approximately half of the known individuals in our study population had previously been marked using uniquely colored radio-collars, it was possible to visually identify some individuals. Subsequent resighting events of marked individuals can be organized into detection histories, similar to mark-recapture data. Combined with sightings of unmarked individuals, these data can then be analyzed in a mark-resight framework (Royle et al. 2014).

Our goal was to evaluate camera trapping and spatial mark-resight methods to estimate Mexican wolf abundance in Arizona. Specifically, our first objective was to evaluate the accuracy and precision of the abundance estimate of Mexican wolves generated from camera trapping and spatial mark-resight methods in relation to the count obtained via the IFT method, which the USFWS Mexican Wolf Recovery Program currently considers the best estimate of population size (USFWS 2020). Our second objective was to compare the equipment and labor costs of estimating Mexican wolf abundance using camera trapping and spatial mark-resight methods to costs associated with the IFT method. Based on the results of our first 2 objectives, our final objective was to recommend best practices for conducting camera trapping to estimate Mexican wolf abundance.

STUDY AREA

The study area (3,532 km^2) was defined as the portion of the MWEPA in Arizona currently occupied by Mexican wolves, buffered by 25.6 km, which is half of the average width of Mexican wolf home ranges (USFWS 2017*c*). We buffered the occupied Mexican wolf area so that our camera grid would include individuals that resided on the edge of the known occupied area. The study area was restricted to MWEPA boundaries and excluded New Mexico and adjacent Fort Apache and San Carlos tribal lands (Figure 1). The study area consisted of lands managed by the U.S. Department of Agriculture-Forest Service (96.8%) in the Apache-Sitgreaves National Forest, with smaller areas of private land (3.0%) and Arizona Game and Fish Commission owned land (0.2%). Mexican wolf prey species in the study area included elk (*Cervus canadensis*), mule deer (*Odocoileous hemionus*), and white-tailed deer (*O. virginianus*; Reed et al. 2006, Martínez-Meyer et al. 2020). Other carnivore species in the study area included black bear (*Ursus americanus*), mountain lion (*Puma concolor*), coyote (*Canis latrans*), and gray fox (*Urocyon cinereoargenteus*).

Elevations ranged from 1,122 m to 3,447 m and topography varied from alpine meadows to steep canyons. The northern half of the study area was primarily composed of southern Rocky Mountain ponderosa pine woodland and

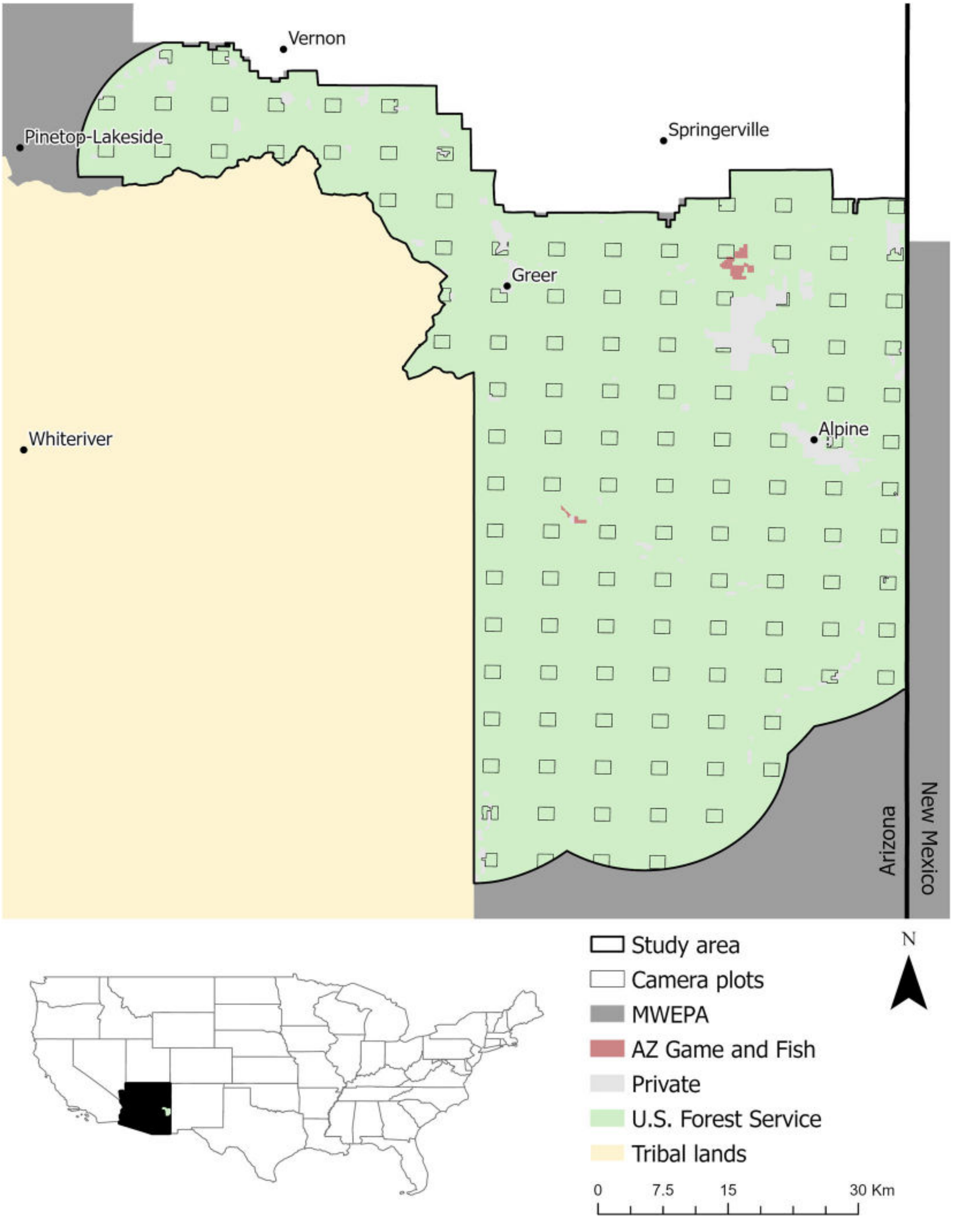

FIGURE 1 Mexican wolf camera trapping study area and land ownership located within the Mexican Wolf Experimental Population Area (MWEPA) in Arizona, USA with 124 1.5-km^2 camera trap plots, placed 5.4 km apart. Camera traps remained in the same locations from November 2019 to July 2020.

montane-subalpine grassland while the southern half was primarily Madrean pinyon-juniper woodland (USGS 2016). Primary overstory species included ponderosa pine (*Pinus ponderosa*), quaking aspen (*Populus tremuloides*), and juniper (*Juniperus* spp.). The majority of rainfall occurred between August–March and the remainder occurred between April–July (mean of 6.1 cm and 2.2 cm, respectively, during 2019–2020; PRISM Climate Group 2021). Snowfall varied by elevation and was greatest in January, ranging from 2.7 cm in the lower elevations to 132.1 cm at the highest elevations during our study period (WRCC 2021). Temperatures ranged from 33.5°C in the summer at low elevations to −10.6°C in the winter at high elevations during our study period (WRCC 2021).

METHODS

Each January since 2006, the IFT has conducted an annual aerial capture operation to collar Mexican wolves (USFWS 2005, 2017*b*). During IFT capture operations, previously collared Mexican wolves were located by telemetry signals from very high frequency (VHF) collars, and associated uncollared pack members were captured via chemical immobilization techniques approved as part of the Mexican Wolf Recovery Plan (USFWS 2017*a*, *b*). The IFT members fitted captured wolves with either a Telonics TGW-4577 or TGW-4477 (Telonics Inc., Mesa, AZ, USA), or Vertex Lite Vectronic (Vectronic Aerospace, Berlin, Germany) combination VHF and global positioning system (GPS) enabled collar. Adults and pups of the most recent spring, regardless of social status, were fitted with collars (USFWS 2020). Single uncollared individuals and individuals of newly formed packs were also opportunistically targeted for collaring. In addition, individuals captured during the year (e.g., depredation conflicts) and adult captive animals that were released between 1998 and 2015, were also fitted with a collar (USFWS 2015*b*, 2017*b*). Collars were programmed to obtain a GPS location every 1 to 13 hours, depending on IFT management needs, and had an operating life of 2–5 years. Collars were not fitted with a release mechanism and therefore remained on the wolves. Each collar was color-coded with a distinctive pattern of tape (hereafter, marked), which allowed for individual collar identification. After approximately 2 to 4 years, the mark deteriorated and exposed the plain collar. The IFT attempted to maintain at least 2 collared individuals per pack (USFWS 2017*b*), and there were at least 40 collared wolves in the study area during our study. Because collaring efforts began in 1998 and occurred annually thereafter, the ≥40 collared individuals present during our study represented a combination of collars with and without distinguishable marks, and collars with and without transmitting telemetry.

Camera trapping was conducted from August 2019 through July 2020. During August and September 2019, we conducted a pilot study to test and refine camera settings and placement configuration to maximize our ability to photograph and identify individual wolves. From the pilot study (see Supporting Information), we concluded that one camera per location, with a sensitivity setting of high and positioned at a height of 80 cm, was the most effective configuration for photographing and identifying wolves. Each camera was also programmed to take 30 photos in 15 seconds with no delay between motion detections. This configuration was used for our full camera trapping survey. We also conducted a computer simulation study to guide our selection of camera trap spacing and to determine the number of cameras to deploy. Our simulation study results suggested that accuracy and precision were improved with more cameras on the landscape (Figure S1, available in Supporting Information).

To maximize the number of cameras on the landscape while considering budget and logistical constraints, we used the fishnet tool in ArcGIS 10.8.1 (ESRI, Redlands, CA, USA) to divide the study area into 124 equally sized grid cells, resulting in 5.4 km^2 cells. To further refine camera placement, we then placed a 1.5 km^2 plot at the center of each grid cell (Figure 1). Between 1 October 2019 and 1 November 2019, we deployed 124 cameras within the central plots by using field observations to select camera locations that would maximize our opportunity for photographing wolves. The selected camera locations included unpaved roads and hiking trails, game trails, areas with Mexican wolf or ungulate sign, and areas such as ridgelines, saddles, and valleys that could funnel wolf movement (Moskowitz and Huyett 2019). We placed approximately one teaspoon of Caven's Quality Animal Gusto skunk scent lure (Minnesota Trapline Products, Pennock, MN, USA) 1.5–2.5 meters in front of each camera trap to improve detection probability and individual identification. We visited each camera trap approximately every 2 weeks to replace batteries, change memory cards, clear any new vegetation, and reapply scent lure.

We divided our survey into 2 seasons based on Mexican wolf phenology. Pups remain near the den for the first 3 months post-parturition (approximately April to June) and enter the mobile population in late summer to early fall (Bednarz 1988, USFWS 2017*c*). Therefore, we defined the winter camera trapping season as 1 November 2019 to 29 February 2020, with the assumption that surviving pups of the year would be available to count by November. We defined the summer survey season as 1 April 2020 to 31 July 2020, designed to start during spring snow melt, when wolves have mostly finished shedding their winter coats, making collars easier to see in photographs. We ended our summer survey at the end of July because new pups are still distinguishable from adults at this time, and can be excluded from photo counts, thereby meeting the demographic closure assumption for mark-resight methods (Royle et al. 2014). While we observed a low level of adult mortality during our surveys, we assumed that abundance estimates corresponding to abundance at the beginning of the survey period would be unbiased if marked and unmarked animals have equal probability of mortality (Otis et al. 1978). Cameras remained in the same locations for both the winter and summer seasons, and we dismantled camera trap stations at the end of the summer survey season.

We identified and counted the number of individuals of all species in the collected photos using Colorado Parks and Wildlife Photo Warehouse software (Ivan and Newkirk 2015). When multiple events of wolves were recorded within 60 minutes, we collapsed these to a single resight event (Meek et al. 2014, Cusack et al. 2015). We identified collared wolves using 2 approaches, initially without and then with the aid of GPS data. We identified wolves without GPS telemetry by using visual reference information, including reference photos of mark (tape) color, pattern, and location on collars, as well as unique natural markings of collared individuals (e.g., one individual with a pendant-shaped ear). After we identified individuals with only visual reference information, we created a second set of encounter histories with the assistance of GPS data. Global positioning system data assisted us in identifying wolves by eliminating distant wolves from consideration. Specifically, we determined the mean minimum 24-hour movement distance for all collared wolves. Then, for each resighting event containing unidentified collared individuals, we eliminated from consideration all wolves outside the mean movement distance of the camera at the time the photo was taken. Our approach reduced the set of candidate wolves, thereby enabling additional positive identifications.

To avoid misidentification of individuals, we only assigned a positive identification when 2 observers were certain of the individual identification. We classified wolves as collared but unidentifiable when a collar was present but the mark was indistinguishable, typically due to photos captured in infrared or faded marks. We classified wolves as uncollared when we could clearly see their neck and a collar was not present. During routine IFT operations, additional animals were collared during our winter survey period. We classified these newly marked individuals as uncollared for our winter datasets to avoid assumption violations. Finally, we classified wolves as uncertain when we could not clearly see their neck, typically due to angle, blur, or distance from the camera. We discarded uncertain records because they do not contribute to the model likelihood when fitting spatial mark-resight models (Efford and Hunter 2017, Augustine et al. 2018). Our sampling process yielded 4 datasets of classified photos: winter and summer datasets developed without the aid of GPS information (hereafter, winter no telemetry and summer no telemetry), and winter and summer datasets developed with the aid of GPS information (hereafter, winter telemetry and summer telemetry).

Spatial mark-resight (SMR) methods use resighting observations from uniquely identifiable individuals and counts of unmarked and marked but unidentifiable individuals to produce a generalized likelihood-based SMR model (Sollmann et al. 2013, Royle et al. 2014, Efford and Hunter 2017). Individual detection probability is modeled using a detection function, which expresses how detection probability declines with increasing distance from an individual's activity center (Rich et al. 2014, Royle et al. 2014). Spatial mark-resight methods model population density as a point process and abundance is derived from the density estimate (Efford and Fewster 2013). Estimated model parameters include density (D), detection probability intercept (h_0), spatial scale parameter (σ), probability of identifying marked individuals (*pID*), and a derived abundance estimate (*N*) for the state space or a smaller, defined region (Efford and Fewster 2013). The state space includes the surveyed area plus a buffer that is large enough so that animals with activity centers outside of the state space boundary have a negligible chance of being photographed by a camera trap, which is important in producing unbiased parameter estimates (Efford and Fewster 2013, Chetri et al. 2019). The state space can further be refined by using a mask to exclude areas of non-habitat and characterize heterogeneous landscapes, which can then be used in model formation to estimate the relationship between model parameters and habitat characteristics and improve abundance estimates (Sharma et al. 2021). A mask can also define a region smaller than the state space if an abundance estimate is desired for a smaller area (Efford and Fewster 2013).

Similar to traditional capture-recapture methods, spatial mark-resight models assume demographic closure, that marks are retained and correctly identified, that the marked population represents a random sample both spatially and demographically within the state space, and that individuals are detected independently (which is tenuous for wolves and further described below; Royle et al. 2014, Sollmann 2018). Also similar to traditional capture-recapture methods, an encounter history is created for each identifiable animal, represented by a sequence of 1's and 0's that reflect sampling occasions during which individuals were or were not detected (Royle et al. 2014). Unlike traditional capture-recapture methods, spatial models account for individual heterogeneity in detection, accommodate study areas that contain unsuitable habitat and boundaries, and can produce more precise estimates (Efford and Fewster 2013, Rich et al. 2014).

We used spatial mark-resight methods (Sollmann et al. 2013, Rich et al. 2014, Royle et al. 2014) to estimate density and abundance of Mexican wolves in Arizona using the secr package version 4.3.3 (Efford 2011) in Program R (version 4.0.3, R Core Team 2020). Our state space included a habitat suitability mask of high- and low-quality Mexican wolf habitat, created for the USFWS Mexican Wolf Recovery Plan (USFWS 2017*a*, Martínez-Meyer et al. 2020). The habitat suitability mask was constructed from climate, land cover, human density, and road density data, and an index of ungulate biomass (Martínez-Meyer et al. 2020). Using the habitat suitability mask, we obtained density estimates for an area that we delineated using Mexican wolf GPS telemetry locations. Specifically, we first used the suggest buffer function in the secr package for each dataset, which provided a buffer width around the trap array (Sharma et al. 2021). We then refined the suggested buffer based on knowledge of Mexican wolf home range locations and IFT operations. Mexican wolves are located in the MWEPA in Arizona and New Mexico and do not reside south of the southern edge of our study area, but are occasionally documented north of the northern edge of our study area. As such, we constrained the south edge of the suggested buffer to our southern study area boundary. To address the north edge of the suggested buffer, we obtained the 95% kernel home range for all wolf GPS locations during our study period using the adehabitatHR package version 0.4.19 (Worton 1989, Calenge 2006). We constrained the north edge of the suggested buffer to include the kernel home range and northern study area boundary, because part of the 95% home range fell slightly outside of our northern study area boundary. Mexican wolves reside to the east and west of our study area and are therefore available to be photographed on our trapping array. Thus, we did not alter the suggested buffer on tribal lands and New Mexico. After the buffer was delineated, which defined the state space, we obtained abundance estimates for our study area, which excluded tribal lands and areas in New Mexico.

To estimate abundance of Mexican wolves, we developed 4 SMR models and used these same models for each of the 4 datasets. Our analyses included 2 models of homogeneous density as well as 2 models where we assessed the potential influence of habitat suitability on density. In one homogenous density model and one heterogeneous density model, we also considered that our ability to identify individuals may be affected by the detection's time of day, because 48% of our data were from infrared photographs, which negatively affected our ability to identify individuals. To account for this heterogeneity in individual identification, we divided each 2 week survey period into day and night hours, so that all day hours during 2 weeks constituted one survey period and all night hours during the same 2 weeks constituted the next survey period. In total, each season included 9, 2 week daytime and 9, 2 week nighttime survey periods. We included a dummy covariate for night survey periods and used this to estimate the effect of night on the probability of identifying marked individuals (*pID*) in 2 of the models. All combinations of these 2 covariates yielded 4 models (Table 1). We compared our 4 models for each dataset using Akaike Information Criterion corrected for small sample size (AIC_c; Burnham et al. 1995). We considered differences in $AIC_c < 2$ as well supported models (Burnham and Anderson 2002, Wagenmakers and Farrell 2004). While sex, social status, dispersal status, and behavioral trap response might affect animal movement or detection, individual covariates cannot be modeled with spatial mark-resight models (Efford 2022).

For each model, we used a half normal detection function, in which we modeled only the resighting process and not the initial marking process (Efford and Hunter 2017). We could not model the marking process because animals were marked via helicopter pursuit or released from captivity. Additionally, an unknown number of marks had been lost since marking first began in 1998 (Royle et al. 2014). Although SMR models that omit a marking model can underestimate density (Murphy et al. 2019), marking occurred randomly in relation to our camera trapping grid and across the extent of our state space. As such, it is reasonable to assume that marked and unmarked animals were equally likely to be detected and therefore, estimates should not be biased if a marking model is not included (Royle et al. 2014, Whittington et al. 2017).

For the top model in each dataset, we also calculated a variance inflation factor and adjusted for overdispersion because wolves demonstrate high levels of aggregation and cohesion due to territoriality and pack association, both

TABLE 1 Candidate spatial mark-resight models of density (*D*), detection probability (h_0), spatial scale parameter (σ), and the probability of identifying individuals that are marked (*pID*) for obtaining abundance estimates of Mexican wolves in Arizona, USA for the winter (November 2019 to February 2020) and summer (April to July 2020) seasons, with and without the aid of telemetry to identify individual wolves. In select models, we accounted for our ability to identify individual wolves in day and night photos through a dummy temporal trap covariate (id), and we also tested the effect of a habitat suitability mask of high- and low-quality Mexican wolf habitat (HS). Models are ranked by Akaike Information Criteria corrected for small sample size (AIC_c) and we report the number of parameters in each model (*K*), difference in AIC_c from the top model (ΔAIC_c), and Akaike weights (ω_i).

Dataset	Model structure	*K*	AIC_c	ΔAIC_c	ω_i
Winter no telemetry	$D(.)\ h_0(.)\ \sigma(.)\ pID(\text{id})$	5	1049.5	0.0	0.81
	$D(\text{HS})\ h_0(.)\ \sigma(.)\ pID(\text{id})$	6	1052.5	3.0	0.18
	$D(.)\ h_0(.)\ \sigma(.)\ pID(.)$	4	1059.3	9.8	0.01
	$D(\text{HS})\ h_0(.)\ \sigma(.)\ pID(.)$	5	1061.9	12.4	0.00
Winter telemetry	$D(.)\ h_0(.)\ \sigma(.)\ pID(\text{id})$	5	1139.7	0.0	0.76
	$D(\text{HS})\ h_0(.)\ \sigma(.)\ pID(\text{id})$	6	1142.0	2.3	0.24
	$D(\text{HS})\ h_0(.)\ \sigma(.)\ pID(.)$	5	1153.1	13.4	0.00
	$D(.)\ h_0(.)\ \sigma(.)\ pID(.)$	4	1154.9	15.1	0.00
Summer no telemetry	$D(.)\ h_0(.)\ \sigma(.)\ pID(\text{id})$	5	1620.8	0.0	0.73
	$D(\text{HS})\ h_0(.)\ \sigma(.)\ pID(\text{id})$	6	1622.9	2.1	0.26
	$D(.)\ h_0(.)\ \sigma(.)\ pID(.)$	4	1629.6	8.7	0.01
	$D(\text{HS})\ h_0(.)\ \sigma(.)\ pID(.)$	5	1631.9	11.0	0.00
Summer telemetry	$D(.)\ h_0(.)\ \sigma(.)\ pID(\text{id})$	5	1706.8	0.0	0.81
	$D(\text{HS})\ h_0(.)\ \sigma(.)\ pID(\text{id})$	6	1709.7	2.9	0.19
	$D(.)\ h_0(.)\ \sigma(.)\ pID(.)$	4	1720.9	14.0	0.00
	$D(\text{HS})\ h_0(.)\ \sigma(.)\ pID(.)$	5	1723.7	16.9	0.00

of which can violate SMR model assumptions regarding independence among detections (Borchers and Efford 2008, López-Bao et al. 2018, Bischof et al. 2020). Aggregation occurs when multiple individuals share activity centers, such as in a wolf pack (Bischof et al. 2020). Cohesion occurs when group members move together, which affects detection patterns, as the probability of detecting one pack member can increase the likelihood of detecting other pack members (Bischof et al. 2020). High overdispersion underestimates variance and therefore decreases confidence interval coverage (Fletcher 2012, Efford and Hunter 2017). Following Bischof et al. (2020), we accounted for overdispersion by inflating variance estimates with Fletcher's $\hat{c}$. After adjusting the confidence intervals for overdispersion, we also measured precision by obtaining the coefficient of variation (CV) for each parameter, and compared the CV values among each dataset (Cappelle et al. 2019, Efford and Boulanger 2019).

We assessed the accuracy of abundance estimates generated by camera trapping by comparing our abundance estimates to the IFT counts because the latter are considered the official population estimate (USFWS 2020). The 2019 IFT minimum count for our winter season was 62 Mexican wolves in Arizona, excluding tribal land. We used a count of 59 Mexican wolves during summer because the IFT recorded 3 mortalities of collared Mexican wolves and zero mortalities of uncollared Mexican wolves in Arizona prior to the summer season (USFWS 2020; J. Greer, AZ Game and Fish Department, personal communication).

To aid managers in selecting between the 2 methods, we compared the expense of camera trapping to the expense of the IFT method. We calculated the expense of equipment and labor of the IFT method for both the first year of implementation and for a standard, subsequent year. Equipment expenses for first year and subsequent IFT counts included helicopter and fixed-wing support, telemetry receivers, and capture equipment such as dart supplies and collars. The IFT labor expenses included hours expended by ground and aerial crews, pre-count preparation, and data analysis. We compared IFT method expenses to the equipment and labor costs required to conduct the camera trapping method for the first year of implementation and for a subsequent year. First year camera trapping equipment expenses included cameras, security enclosures, cable locks, memory cards, lithium batteries, and scent lure. First year camera trapping labor hours included placing, checking, and removing cameras, as well as the time required for photo processing, individual wolf identification, and performing statistical analysis. Subsequent year camera trapping equipment expenses included lithium batteries and scent lure. Camera trapping expenses were calculated based on the actual expenses that were incurred (hereafter, incurred), including extra equipment in case of theft, and separately, expenses based on our recommendations for best practices and greatest efficiency (hereafter, improved). Improved labor hours include identifying photos of wolves (i.e., not all species), reducing the number of photos recorded per motion activation, and reducing the number of visits to cameras. Improved equipment expenses include lure requirements from reduced camera services. The expense of capturing and marking wolves was included in both the IFT method and camera trapping method because both currently rely on collared wolves. We did not include the expense of vehicle operation and maintenance due to the potential variability across wildlife management agencies and proximity to field locations. Cost estimates were based on current Mexican wolf distribution in Arizona, excluding tribal land, and as such, reflect the effort necessary to survey 3,532 km^2.

RESULTS

Camera traps operated 36–121 days in winter ($\bar{x}$ = 116 days, SD = 13.6) and 47–122 days in summer ($\bar{x}$ = 117 days, SD = 11.9). Days of operation varied among cameras due to battery life, memory card usage, or because some cameras were checked less frequently due to remote locations or deep snow. Additionally, one camera and its memory card were destroyed in a wildfire, and 4 cameras were stolen (and replaced upon discovery). We collected 7,063,180 photos across 2 survey seasons. We collected 2,177,793 photos in winter, 7,715 of which included wolves in 114 independent events (54 at night and 60 during day). We collected 4,885,387 photos in summer, 5,602 of which included wolves in 130 independent events (64 at night and 66 during day). We recorded approximately twice as many positively identified wolf resightings in summer, compared to winter (Table 2). As such, summer telemetry was our largest dataset with 100 positively identified resightings of 37 unique Mexican wolves (Table 2).

The most supported model for all 4 datasets was when *pID* varied by time of day, due to a lower ability to identify individuals at night (Table 1). The winter no telemetry dataset produced an abundance estimate of 33 Mexican wolves (95% CI = 15–52 individuals, CV = 0.28), which was below the IFT count of 62 individuals (Figure 2). The winter telemetry dataset produced an abundance estimate of 45 Mexican wolves (95% CI = 28–62 individuals, CV = 0.19), which captured the IFT count (62 individuals) in the 95% confidence interval (Figure 2). The abundance estimate for the summer no telemetry dataset was 43 Mexican wolves (95% CI = 30–56 individuals,

TABLE 2 The number of Mexican wolves positively identified to individual, the number of unique Mexican wolves from those positively identified, as well as collared but unidentifiable (unID), uncollared, and uncertain classifications for each study season with and without the assistance of GPS telemetry to identify individuals. Winter camera trapping data were collected from November 2019 to February 2020 in the Mexican Wolf Experimental Population Area (MWEPA) in Arizona, USA. Summer camera trapping data were collected from April 2020 to July 2020 at the same locations.

	Winter		Summer	
Category	No telemetry	Telemetry	No telemetry	Telemetry
Positively ID	29	50	73	100
Unique ID	14	22	31	37
Collared unID	63	42	78	51
Uncollared	78	78	50	50
Uncertain	42	42	28	28

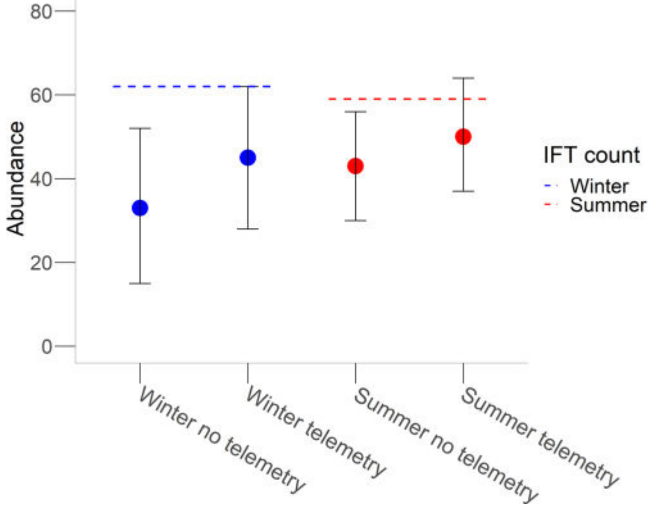

FIGURE 2 Spatial mark-resight Mexican wolf abundance estimates with lower and upper 95% confidence intervals for each dataset, as well as the Interagency Field Team (IFT) count for each season. The winter season was defined as November 2019 to February 2020 and the summer season was defined as April 2020 to July 2020. Abundance estimates are for the Mexican Wolf Experimental Population Area (MWEPA) in Arizona, USA, excluding tribal land.

CV = 0.16), which was below the IFT count of 59 individuals (Figure 2). The summer telemetry dataset produced an abundance estimate of 50 Mexican wolves (95% CI = 37–64 individuals, CV = 0.13), which was 14% below the IFT count (59 individuals) but captured the IFT count in the 95% confidence interval (Figure 2). Our ability to identify marked individuals with the summer telemetry dataset was 0.77 (95% CI = 0.58–0.88, CV = 0.10), which was the largest identification probability among the 4 datasets (Table 3). Both summer datasets had greater precision than winter datasets and the use of telemetry improved the accuracy of estimates. Fletcher's $\hat{c}$ ranged from 1.68 (winter no telemetry) to 2.77 (summer telemetry), indicating a degree of overdispersion and therefore underestimation of variance (Bischof et al. 2020). We used Fletcher's $\hat{c}$ to inflate variance estimates and report only the corrected confidence intervals (Bischof et al. 2020).

We calculated camera trapping expenses based on our summer telemetry dataset because the abundance estimate was closest to the IFT count and most precise. Camera trapping had an initial expense for equipment ($149,468), which was reduced (69% decrease) for subsequent years (Table 4; Table S1 and Table S2, available in

TABLE 3 Spatial mark-resight parameter estimates, lower and upper 95% confidence intervals, and coefficient of variation (CV) for each top model for each combination of season and GPS telemetry dataset. Parameter estimates include density (D, Mexican wolves/100 km^2), detection probability (h_0), spatial scale parameter (σ, km), and the probability of identifying individuals that are marked (pID). Mexican wolf camera trapping abundance estimates ($\hat{N}$) reflect estimates for the winter season, November 2019 to February 2020, and the summer season, April 2020 to July 2020, in the Mexican Wolf Experimental Population Area (MWEPA) in Arizona, USA, excluding tribal land.

Dataset	Parameter	Estimate	Lower CI	Upper CI	CV
Winter no telemetry	D	0.95	0.56	1.61	0.28
Fletcher's $\hat{c}$ = 1.68	h_0	0.13	0.05	0.28	0.45
	σ	3.40	2.30	5.02	0.20
	pID	0.49	0.35	0.62	0.14
	$\hat{N}$	33	15	52	0.28
Winter telemetry	D	1.29	0.79	2.08	0.26
Fletcher's $\hat{c}$ = 2.22	h_0	0.07	0.03	0.14	0.39
	σ	3.98	2.90	5.46	0.16
	pID	0.72	0.53	0.85	0.11
	$\hat{N}$	45	28	62	0.19
Summer no telemetry	D	1.23	0.85	1.80	0.20
Fletcher's $\hat{c}$ = 2.47	h_0	0.06	0.03	0.10	0.33
	σ	4.73	3.58	6.26	0.14
	pID	0.57	0.41	0.71	0.14
	$\hat{N}$	43	30	56	0.16
Summer telemetry	D	1.43	0.98	2.09	0.20
Fletcher's $\hat{c}$ = 2.77	h_0	0.05	0.03	0.09	0.29
	σ	4.64	3.68	5.86	0.12
	pID	0.77	0.58	0.88	0.10
	$\hat{N}$	50	37	64	0.13

TABLE 4 Camera trapping and IFT expenses for a first year and a standard year after the first (subsequent year), categorized by equipment expenses ($USD) and labor hours. Camera trapping expenses reflect the cost to obtain abundance estimates of Mexican wolves in Arizona, USA (Incurred) as well as camera trapping expenses if our recommendations for best practices and greatest efficiency were implemented (Improved). The approximate expenses of the IFT method reflects the equipment expenses and labor hours that are required to obtain a minimum known population count of Mexican wolves in Arizona. All monetary expenses reflect market value from November 2019 to July 2020.

	Camera trapping method				IFT method	
	First		Subsequent		Incurred	
	Incurred	Improved	Incurred	Improved	First	Subsequent
Equipment	$149,468	$148,484	$88,224	$87,783	$86,570	$86,570
Labor hours	3,852	1,178	3,852	1,178	824	824

Supporting Information). Camera trapping labor hours for the first year and for each subsequent year remained the same (3,852 hours), but decreased by 69% if our recommendations are implemented (Table S3, available in Supporting Information). The IFT method required recurring equipment expenses which were consistent between the first year and each subsequent year ($86,570; Table S4, available in Supporting Information), and were 73% less than first year camera trapping expenses and similar to both incurred and improved subsequent year camera trapping expenses (Table 4). The IFT labor hours were 43% (improved labor hours) to 78% (incurred labor hours) less than the camera trapping labor hours (Table 4; Table S5, available in Supporting Information).

DISCUSSION

Our study focused on the evaluation of camera trapping methods for estimating Mexican wolf abundance. Our first objective was to evaluate the accuracy and precision of using camera traps to estimate Mexican wolf abundance by comparing the abundance estimate generated from camera trapping to the IFT count. The low abundance estimates for all 4 datasets may be due to low individual identification, demographic stochasticity, or possible assumption violations such as closure and independence (further described below). Importantly, the IFT count, which is the official population estimate and benchmark against which we compared camera trapping estimates, is potentially biased low due to the possibility of detection probability <1. Therefore, the camera trapping estimates may be more biased than we report.

Our second objective was to compare the equipment costs and labor hours of estimating Mexican wolf abundance with camera trapping to those associated with the IFT method. Because the cost of capture represents 58–98% of the camera trapping expenses, marking expenses should be minimized for cost effective camera trapping. Although a reduction in marking expenses would also reduce expenses for the IFT method, permanent marks may drastically reduce camera trapping expenses. Additionally, if implementing permanent marks, collaring every other year, rather than every year, may also reduce marking expenses. Because the CV was less than 15% for the summer telemetry dataset, marking animals every other year could potentially maintain precision <20%, which could still detect changes in population growth (Pollock et al. 1990, Whittington et al. 2017).

Our final objective was to recommend best methodological practices for conducting camera trapping to estimate Mexican wolf abundance. First, we do not recommend camera trapping during the winter due to inaccurate and imprecise estimates. We obtained fewer Mexican wolf events in the winter and detected individuals were not resighted as frequently as in the summer datasets. Without adequate resighting events, the estimation of activity centers is biased and model parameters can become inestimable (Sollmann et al. 2013, Royle et al. 2014). Our ability to identify marked individuals during winter was diminished compared to summer, and the accuracy and precision of SMR parameter estimates are dependent on the number of marked individuals in the population and the observer's ability to correctly identify marks (Sollmann et al. 2013, Royle et al. 2014). Low individual identification in the winter could be due to Mexican wolf winter coats obscuring the collar marks. Because of the reduced ability to identify individuals in winter, which likely contributed to inaccurate and imprecise estimates, we do not recommend camera trapping during this season.

Our second recommendation is to investigate delaying the summer camera trapping season from April–August to May–August. Specifically, camera trapping abundance estimates that are biased low may also be due to violations of SMR model assumptions. Wolves are generally aggregated due to pack association and tend to become more aggregated in the spring due to pup rearing (Bednarz 1988), which violates the assumption of independence among activity centers (Bischof et al. 2020). High levels of aggregation and cohesion can result in biased-low population estimates, but primarily decreases confidence interval coverage (López-Bao et al. 2018, Bischof et al. 2020). Although we adjusted our confidence intervals for overdispersion, the effects of non-independence have not been tested for Mexican wolves and, therefore, may have still biased our parameter estimates, particularly with the summer datasets as Fletcher's $\hat{c}$ was larger than in the winter datasets.

Although parameter estimates were low for all 4 datasets, we provide the following methodological recommendations for Mexican wolf camera trapping for future research. First, we recommend experimenting with longer durations between camera checks. The majority (97%) of our camera traps functioned beyond 5 months without requiring a battery service. Cameras that required new batteries typically had excessive vegetation growth between service dates, which can generally be avoided by placing large rocks to discourage growth or facing cameras away from established vegetation. By servicing each camera trap only once instead of approximately every 2 weeks during a season, we could have saved 1,120 labor hours during one season. Second, we recommend expediting the species identification process. We uploaded all 4,885,387 summer photos into a photo database and identified and counted the number of all animal species in each photo, which required approximately 1,628 labor hours. To efficiently target events of wolves, we recommend that users first view photos in a photo viewer program and extract only photos of wolves, which would have saved 1,479 hours for >4.5 million photos. Third, we recommend investigating use of artificial intelligence software as an alternative to manual extraction and identification of photos (Schneider et al. 2019). We investigated artificial intelligence to aid in species identification but the available options did not appear cost effective at the time of our study. We did not calculate the labor hours associated with artificial intelligence in our cost estimation but artificial intelligence photo identification software may prove cost-effective for a larger or longer-term effort, such as the Mexican wolf monitoring considered here. Fourth, we found that our ability to identify individuals did not improve beyond 15 photos. Therefore, the number of photos per motion activation can be reduced to 15, which would reduce the wolf photo extraction process to approximately 75 hours. Fifth, and perhaps most important, many of the events that required more than 5 photos to identify an individual often had a deteriorated collar mark (i.e., the tape was faded or removed) or the photo was captured in infrared. Precision typically improves with more marked animals in the population (Whittington et al. 2017) and, although approximately half of the study population was collared, many marks were deteriorated. We therefore recommend a more permanent marking method and using a mark that is distinguishable in monochrome infrared photos. We recommend experimentation with a marked numbering system, permanent paint with distinct patterns, or potentially numbered ear tags. If using a color marking system, we recommend that users record reference photos of marks in both day and infrared light, possibly by using a camera trap in a controlled setting prior to collaring operations. Improvements to the marking system will reduce the number of photos needed in each resighting event and yield positive identifications in more resighting events, which should improve parameter accuracy, parameter precision, and reduce labor costs of camera trap servicing and photo identification.

Although spatial mark-resight models may have the potential to produce reliable Mexican wolf abundance estimates, alternative analytical approaches may prove successful for long-term monitoring and may not require improvements to the marking system. For example, camera trapping with space-to-event models have recently produced abundance estimates for gray wolves in Idaho (Ausband et al. 2022). Space-to-event models do not require individually marked animals and do not require a high-density survey effort (Ausband et al. 2022). Models with individual identification are typically more precise than unmarked models (Morin et al. 2022), but the precision of some space-to-event models are comparable to the precision of our estimates (Moeller et al. 2018, Ausband et al. 2022). Space-to-event models have also been successfully implemented in landscapes >10,000 km^2 (Ausband et al. 2022), which will be important if the Mexican wolf population continues to increase in abundance and expand geographically. Occupancy models may also provide an approach for estimating wolf abundance without the need for individual identification and can include information such as data from big-game hunter surveys, howl, or sign surveys (Ausband et al. 2014, Garland et al. 2020, Sells et al. 2020). Occupancy models can also be implemented over large extents and be less labor intensive than using camera traps (Garland et al. 2020). Although occupancy and space-to-event models have been used to estimate wolf abundance, both techniques may lack the ability to detect small changes in abundance, which will be necessary for the recovery of the Mexican wolf. Therefore, although unmarked techniques are potential options for long-term monitoring, accurate and precise abundance estimates are likely more obtainable with individually identifiable analysis methods, such as the spatial mark-resight methods discussed here, in particular if recommended improvements are implemented.

MANAGEMENT IMPLICATIONS

Many wildlife agencies continue to investigate methods for obtaining reliable abundance estimates of wolves while minimizing the time, effort, and cost of surveys. The IFT method is constrained by time, effort, and cost challenges that will likely increase if the Mexican wolf population continues to grow. Our analysis suggests that camera trapping with SMR methods is also met with challenges of accuracy, precision, and cost. For managers interested in continuing to experiment with camera traps to estimate Mexican wolf abundance, we provided recommendations that may improve the accuracy of abundance estimates and reduce survey expenses and labor costs. Ultimately, the selection of methods will depend on a manager's budget, staffing capabilities, and time allocation, as well as the precision and accuracy needed for their management decisions. The results of our project provide information on the cost and reliability of camera trapping methods, to help a manager make the most appropriate decision for their population monitoring needs.

ACKNOWLEDGMENTS

We thank C. G. Aymami, M. L. Crabb, R. L. Harrow, T. B. Roderick, and P. J. Teetsel, Arizona Game and Fish Department, as well as numerous trained volunteers who assisted us with identifying over 7 million photos. We also thank J. P. Greer, G. E. Fuller, and J. A. Black, Arizona Game and Fish Department, for providing us with expertise, assistance, and materials to identify individual wolves. We are also grateful to J. C. deVos and J. R. Heffelfinger for review of an earlier version of this manuscript. Camera trapping research was funded through the Federal Aid in Wildlife Restoration Act. The IFT personnel and operations were funded through Section 6 for endangered species conservation, U.S. Fish and Wildlife Service cooperative agreements, and Heritage Fund IIAPM.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

This research was conducted to support the Mexican Wolf Recovery Plan, First Revision (USFWS 2017*a*) and was approved through an Arizona Game and Fish Department study plan and Environmental Assessment Checklist, number M16-1014035121.

DATA AVAILABILITY STATEMENT

Authors elect to not share data due to sensitivity of the focal species.

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REFERENCES

Alisauskas, R. T., R. F. Rockwell, K. W. Dufour, E. G. Cooch, G. Zimmerman, K. L. Drake, J. O. Leafloor, T. J. Moser, and E. T. Reed. 2011. Harvest, survival, and abundance of midcontinent lesser snow geese relative to population reduction efforts. Wildlife Monograph 179:1–42.

Augustine, B. C., F. E. C. Stewart, J. A. Royle, J. T. Fisher, and M. J. Kelly. 2018. Spatial mark-resight for categorically marked populations with an application to genetic capture-recapture. bioRxiv. https://doi.org/10.1101/299982

Ausband, D. E., P. M. Lukacs, M. Hurley, S. Roberts, K. Strickfaden, and A. K. Moeller. 2022. Estimating wolf abundance from cameras. Ecosphere 13:e3933.

Ausband, D. E., L. N. Rich, E. M. Glenn, M. S. Mitchell, P. Zager, D. A. W. Miller, L. P. Waits, B. B. Ackerman, and C. M. Mack. 2014. Monitoring gray wolf populations using multiple survey methods. Journal of Wildlife Management 78:335–346.

Bednarz, J. C. 1988. The Mexican wolf: biology, history, and prospects for reestablishment in New Mexico. University of New Mexico. Albuquerque, USA.

Bischof, R., P. Dupont, C. Milleret, J. Chipperfield, and J. A. Royle. 2020. Consequences of ignoring group association in spatial capture-recapture analysis. Wildlife Biology 1:1–10.

Bogan, M. A., and P. Melhop. 1983. Systematic relationships of gray wolves (*Canis lupus*) in southwestern North America. Occasional Papers: The Museum of Southwestern Biology 1:1–21.

Borchers, D. L., and M. G. Efford. 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. Biometrics 64:377–385.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Second Edition. Springer, New York, New York, USA.

Burnham, K. P., G. C. White, and D. R. Anderson. 1995. Model selection strategy in the analysis of capture-recapture data. Biometrics 51:888–898.

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.

Cappelle, N., M. Després-Einspenner, E. J. Howe, C. Boesch, and H. S. Kühl. 2019. Validating camera trap distance sampling for chimpanzees. American Journal of Primatology 81:e22962.

Chetri, M., M. Odden, K. Sharama, O. Flagstad, and P. Wegge. 2019. Estimating snow leopard density using fecal DNA in a large landscape in north-central Nepal. Global Ecology and Conservation 17:e00548.

Cusack, J. J., A. J. Dickman, J. M. Rowcliffe, C. Carbone, D. W. Macdonald, and T. Coulson. 2015. Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. PLoS ONE 10:e0126373.

Efford, M. 2011. Estimation of population density by spatially explicit capture-recapture analysis of data from area searches. Ecology 92:2202–2207.

Efford, M. 2022. secr 4.3 - spatially explicit capture-recapture in R. https://cran.r-project.org/web/packages/secr/vignettes/secr-overview.pdf

Efford, M., and J. Boulanger. 2019. Fast evaluation of study designs for spatially explicit capture-recapture. Methods in Ecology and Evolution 9:1529–1535.

Efford, M. G., and R. M. Fewster. 2013. Estimating population size by spatially explicit capture-recapture. Oikos 122: 918–928.

Efford, M. G., and C. M. Hunter. 2017. Spatial capture-mark-resight estimation of animal population density. Biometrics 74: 411–420.

Fletcher, D. J. 2012. Estimating overdispersion when fitting a generalized linear model to sparse data. Biometrika 99: 230–237.

Fryxell, J. M., A. R. E. Sinclair, and G. Caughley. 2014. Wildlife ecology, conservation, and management. Third Edition. John Wiley and Sons Ltd, West Sussex, UK.

García-Moreno, J., M. D. Matocq, M. S. Roy, E. Geffen, and R. K. Wayne. 1996. Relationships and genetic purity of the endangered Mexican wolf based on analysis of microsatellite loci. Conservation Biology 10:376–389.

Garland, L., A. Crosby, R. Hedley, S. Boutin, and E. Bayne. 2020. Acoustic vs. photographic monitoring of gray wolves (*Canis lupus*): a methodological comparison of 2 passive monitoring techniques. Canadian Journal of Zoology 98:219–228.

Gerber, B. D., J. S. Ivan, and K. P. Burnham. 2014. Estimating the abundance of rare and elusive carnivores from photographic-sampling data when the population size is very small. Population Ecology 56:463–470.

Ivan, J. S., and E. S. Newkirk. 2015. CPW Photo Warehouse: a custom database to facilitate archiving, identifying, summarizing, and managing photo data collected from camera traps. Methods in Ecology and Evolution 7:499–504.

Jacobs, C. E., and D. E. Ausband. 2018. An evaluation of camera trap performance—what are we missing and does deployment height matter? Remote Sensing in Ecology and Conservation 4:352–360.

Kahn, J. E., C. Hager, J. C. Watterson, N. Mathies, and K. J. Hartman. 2019. Comparing abundance estimates from closed population mark-recapture models of endangered adult Atlantic sturgeon. Endangered Species Research 39:63–76.

López-Bao, J. V., R. Godinho, C. Pacheco, F. J. Lema, E. García, L. Llaneza, V. Palacios, and J. Jiménez. 2018. Toward reliable population estimates of wolves by combining spatial capture-recapture models and non-invasive DNA monitoring. Scientific Reports 8:1–8.

Marnewick, K., P. J. Funston, and K. U. Karanth. 2008. Evaluating camera trapping as a method for estimating cheetah abundance in ranching areas. South African Journal of Wildlife Research 38:59–65.

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. 2020. Rangewide habitat suitability analysis for the Mexican wolf (*Canis lupus baileyi*) to identify recovery areas in its historical distribution. Biodiversity Research 27:642–654.

Meek, P. D., G. Ballard, A. Claridge, R. Kays, K. Moseby, T. O'Brien, A. O'Connell, J. Sanderson, D. E. Swann, M. Tobler, et al. 2014. Recommended guiding principles for reporting on camera trapping research. Biodiversity and Conservation 23: 2321–2343.

Moeller, A. K., P. M. Lukacs, and J. S. Horne. 2018. Three novel methods to estimate abundance of unmarked animals using remote cameras. Ecosphere 9:e02331.

Morin, D. J., J. Boulanger, R. Bischof, D. C. Lee, D. Ngoprasert, A. K. Fuller, B. McLellan, R. Steinmetz, S. Sharma, D. Garshelis, et al. 2022. Comparison of methods for estimating density and population trends for low-density Asian bears. Global Ecology and Conservation 35:e02058.

Moskowitz, D., and A. Huyett. 2019. Citizen Wildlife Monitoring Project. Wolf remote camera traps: scouting guidelines and installation protocol. <https://www.conservationnw.org/wp-content/uploads/2017/06/Wolf-Remote-Camera-Trap-Guidelines-2019.docx.pdf>. Accessed 11 July 2019.

Murphy, S. M., D. T. Wilckens, B. C. Augustine, M. A. Peyton, and G. C. Harper. 2019. Improving estimation of puma (*Puma concolor*) population density: clustered camera-trapping, telemetry data, and generalized spatial mark resight models. Scientific Reports 9:4590.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62:3–315.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107:3–97.

PRISM Climate Group, Oregon State University. 2021. Data explorer. <http://prism.oregonstate.edu>. Accessed 7 July 2021.

R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

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.

Rich, L. N., M. J. Kelly, R. Sollmann, A. J. Noss, L. Maffei, R. L. Arispe, A. Paviolo, C. D. De Angelo, Y. E. Di Blanco, and M. S. Di Bitetti. 2014. Comparing capture-recapture, mark-resight, and spatial mark-resight models for estimating puma densities via camera traps. Journal of Mammalogy 95:382–391.

Rovero, F., and A. R. Marshall. 2009. Camera trapping photographic rate as an index of density in forest ungulates. Journal of Applied Ecology 46:1011–1017.

Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2014. Spatial capture-recapture. Academic Press, Waltham, Massachusetts, USA.

Schneider, S., G. W. Taylor, S. Linquist, and S. C. Kremer. 2019. Past, present and future approaches using computer vision for animal re-identification from camera trap data. Methods in Ecology and Evolution 10:461–470.

Sells, S. N., A. C. Keever, M. S. Mitchell, J. Gude, K. Podruzny, and R. Inman. 2020. Improving estimation of wolf recruitment and abundance, and development of an adaptive harvest management program for wolves in Montana. Final report for federal aid in wildlife restoration grant W-161-R-1. Montana Fish, Wildlife and Parks, Helena, USA.

Sharma, R. K., K. Sharma, D. Borchers, Y. V. Bhatnagar, K. R. Suryawanshi, and C. Mishra. 2021. Spatial variation in population-density of snow leopards in a multiple use landscape in Spiti Valley, Trans-Himalaya. PLoS ONE 16:e0250900.

Silver, S. C., L. E. T. Ostro, L. K. Marsh, L. Maffei, A. J. Noss, M. J. Kelly, R. B. Wallace, H. Gomez, and G. Ayala. 2004. The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. Oryx 38: 148–154.

Sollmann, R. 2018. A gentle introduction to camera-trap data analysis. African Journal of Ecology 56:740–749.

Sollmann, R., B. Gardner, A. W. Parsons, J. J. Stocking, B. T. McClintock, T. R. Simons, K. H. Pollock, and A. F. O'Connell. 2013. A spatial mark-resight model augmented with telemetry data. Ecology 94:553–559.

Takashina, N., B. Kusumoto, M. Beger, S. Rathnayake, and H. P. Possingham. 2018. Spatially explicit approach to estimation of total population abundance in field surveys. Journal of Theoretical Biology 453:88–95.

Trolle, M., and M. Kéry. 2003. Estimation of ocelot density in the Pantanal using capture-recapture analysis of camera-trapping data. Journal of Mammalogy 84:607–614.

U.S. Fish and Wildlife Service [USFWS]. 2005. Mexican wolf recovery program: progress report No. 8. Reporting period: January 1–December 31, 2005.

U.S. Fish and Wildlife Service [USFWS]. 2015*a*. Endangered and threatened wildlife and plants; endangered status for the Mexican wolf and regulations for the nonessential experimental population of the Mexican wolf; final rule. Federal Register 80:2488–2512.

U.S. Fish and Wildlife Service [USFWS]. 2015*b*. Mexican wolf recovery program: progress report No. 18. Reporting period: January 1–December 31, 2015.

U.S. Fish and Wildlife Service [USFWS]. 2017*a*. Mexican wolf recovery plan, first revision. Region 2, Albuquerque, New Mexico, USA.

U.S. Fish and Wildlife Service [USFWS]. 2017*b*. Mexican wolf recovery implementation strategy. Region 2, Albuquerque, New Mexico, USA.

U.S. Fish and Wildlife Service [USFWS]. 2017*c*. Mexican wolf biological report: version 2. Region 2, Albuquerque, New Mexico, USA.

U.S. Fish and Wildlife Service [USFWS]. 2020. Mexican wolf recovery program monthly updates: January 1–31, 2020 to April 1–30, 2020. Region 2, Albuquerque, New Mexico, USA.

U.S. Fish and Wildlife Service [USFWS]. 2022. Mexican wolf recovery program quarterly update: first quarter, 2022 (January, February, March).

U.S. Geological Survey [USGS]. 2016. LANDFIRE existing vegetation type layer. <https://www.landfire.gov/evt.php>. Accessed 26 July 2019.

vonHoldt, B. M., J. P. Pollinger, D. A. Earl, J. C. Knowles, A. R. Boyko, H. Parker, E. Geffen, M. Pilot, W. Jedrzejewski, B. Jedrzejewska, et al. 2011. A genome-wide perspective on the evolutionary history of enigmatic wolf-like canids. Genome Research 21:1234–1305.

Wagenmakers, E., and S. Farrell. 2004. AIC model selection using Akaike weights. Psychonomic Bulletin and Review 11: 192–196.

Welbourne, D. J., C. MacGregor, D. Paul, and D. B. Lindenmayer. 2015. The effectiveness and cost of camera traps for surveying small reptiles and critical weight range mammals: a comparison with labour-intensive complementary methods. Wildlife Research 42:414–425.

Western Regional Climate Center [WRCC]. 2021. Arizona NOAA cooperative stations - temperature and precipitation cooperative climatological data summaries. <https://wrcc.dri.edu/summary/Climsmaz.html>. Accessed 7 July 2021.

Whittington, J., M. Hebblewhite, and R. B. Chandler. 2017. Generalized spatial mark-resight models with an application to grizzly bears. Journal of Applied Ecology 55:157–168.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, California, USA.

Witmer, G. W. 2005. Wildlife population monitoring: some practical considerations. Wildlife Research 32:259–263.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Associate Editor: J. Hinton.

SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

How to cite this article: Russo, B. M., A. S. Jones, M. J. Clement, N. Fyffe, J. I. Mesler, and E. S. Rubin. 2023. Camera trapping as a method for estimating abundance of Mexican wolves. Wildlife Society Bulletin 47:e1416. https://doi.org/10.1002/wsb.1416