DEVELOPING A MANAGEMENT TOOL TO ESTIMATE UNMARKED PUMA (PUMA CONCOLOR) POPULATIONS WITH A REMOTE CAMERA ARRAY

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DEVELOPING A MANAGEMENT TOOL TO ESTIMATE UNMARKED PUMA
(PUMA CONCOLOR) POPULATIONS WITH A REMOTE CAMERA ARRAY

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Wildlife and Fisheries Biology

by
Megan Elise Pitman
August 2010

Accepted by:
Dr. Joseph Lanham, Committee Chair
Dr. Travis Perry
Dr. Patrick Gerard
ABSTRACT

Puma (Puma concolor) ecological research, puma management, and puma conservation require a technique to efficiently estimate puma populations. Adequate population estimates for pumas are difficult to produce due to natural history characteristics of the species. Remote camera arrays present a promising new tool for surveying cryptic mammals, but techniques for estimating population levels of unmarked animals or species that are difficult to individually identify in photographs are needed. Our goal was to develop techniques to (1) determine the camera effort needed to detect resident pumas with 95% certainty and (2) estimate puma population density for unmarked pumas with a remote camera array. An array of 25 cameras spread 2 km apart in a square grid covering an area of 100 km$^2$ was used to detect 5 individually marked pumas. Photographic captures and GPS collar data for 1 male and 1 female puma were used to calculate the mean number of camera days required to reach a detection probability of 95% for a single resident puma within a camera array of one to 25 cameras. These photographic capture rates were used to calculate population density estimates based on how many cameras were used in the array, how many camera nights were included in the survey, and how many total puma photos were captured. Population estimates were calculated based on puma photos from 71 continuous running days of a 25 camera array from November 11, 2009 to January 20, 2010 and included a total of 1188 camera nights. A mark-resight population estimate yielded a puma density of 2.1 (1.7-4.4) puma/100 km$^2$. Our population estimate based on photo capture rate yielded 1.8 (1.4-2.2) puma/100 km$^2$ and fell within the 95% confidence interval of the mark-resight
estimate. These results suggest that remote camera arrays can be used to accurately estimate resident puma population density based on the number of unmarked puma photos captured.
DEDICATION

For myself, mountain lions, and my very supportive family.
ACKNOWLEDGMENTS

I would like to first thank Dr. Travis Perry, my research advisor, who orchestrated this project, providing countless hours of help and support throughout the entire process, and Dr. Drew Lanham, my committee chair, who gave me the opportunity to pursue this research with him at Clemson University. The complexities of my data analysis were mostly handled by Dr. Patrick Gerard and Dr. Katherine Thibault who were both instrumental in developing SAS and R programs, respectively, making my data analysis possible.

Special thanks to all of our funding sources including but not limited to Furman University, the Oregon Zoo, and the Cougar Network. Thanks also to the amazing Ladder Ranch and its staff for hosting our research and providing sometimes much needed logistical support. Speaking of logistics, much of the data would have been lost or not collected if not for the volunteer camera checking efforts of Harley Shaw and his wife Patty Woodruff who maintained the camera grid when there was no one else on site to do so. I appreciate all those who helped with and learned from the fieldwork for this project including Furman HHMI and Wild Semester students.
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INTRODUCTION

Effective management and conservation of any species requires a detailed planning process that identifies specific goals. The first critical goal is to determine the population size and distribution of the species in question. The degree of detail desired in population data varies widely from the simple documentation of species presence for the conservation of rare and endangered species to details of population demographics for the management of game species. Some individual species may fall into both categories depending on location. Puma (*Puma concolor*), for example, are considered big game species in much of the western United States, but an extirpated or endangered species in the Mid-west and Florida respectively. For rare and endangered species there is particular value placed on techniques for which probability of detection can be calculated confidently from survey effort. For large game species in the western United States, such as deer, elk, bighorn sheep, mountain goats, and pronghorn, direct visual surveys may be accomplished from aircraft (Ref). In the eastern U.S., visual counts may be accomplished with spotlight surveys from vehicles (Collier 2007), but much of the population data on eastern cervids is gathered using indirect methods, such as hunter success and harvest demographics (Carpenter 2000). Indirect survey methods are also the most common avenue for obtaining population data on carnivores, which typically occur at much lower population densities and are more secretive than ungulates. The natural history of larger carnivore species exacerbates the difficulties inherent in gathering population data as they occur at the lowest population densities, often in remote and difficult to access terrain, and may be particularly wary of human presence.
In North America, large felids, such as jaguar and puma, are particularly difficult to study in this regard (Logan & Sweanor 2001; McCain & Childs 2008). Population density estimates for pumas in particular are difficult to produce using common population assessment techniques due to ecological characteristics of pumas, including their naturally low population densities, extensive ranges, cryptic nature, and relatively uniform coloration (Logan & Sweanor 2001). In the last few decades there has been growing interest in the management and conservation of puma and jaguar (Anderson et al. 2010; McCain & Childs 2008). Since the late 1960’s, as puma were reclassified from vermin to big game species in many western states and to a federally endangered species in Florida, a wide range of study techniques have been developed for this elusive carnivore, particularly techniques used to gather population data (Shaw 2010).

In general, these survey techniques can be classified as either “invasive” or “non-invasive”. MacKay et al. (2008b) provide an explanation of these two potentially misleading terms. Essentially, invasive techniques either require or have significant potential for human interaction with the study species, such as telemetry studies, which may alter natural behavior. Non-invasive techniques do not require human interaction with the species and are considered to be “remote”. Using trail cameras to survey the species that occur in an area is an example of a non-invasive technique. MacKay et al. (2008b) are careful to point out that there may be an overlap because some non-invasive techniques may still disrupt normal behavior of the study species, such as the flash from a remote camera. Non-invasive survey techniques are particularly well suited to carnivores given the significant costs in time and effort required to locate and capture individuals.
versus the relatively lower costs of surveys for sign or, again, the checking of trail cameras.

There are two commonly used methods of population estimation that utilize harvest data and may be considered to have broad overlap in both the invasive and non-invasive categories. They are: (1) the use of demographic data and (2) location data recorded from harvested pumas. These data may be used in at least two ways. First, demographic data may be used to indicate whether a population is a sink or a source (population declining vs. stable or increasing). Second, location data from harvested puma may be used with GIS technology to construct habitat suitability models for a region or state. The first strategy may be problematic as data can produce ambiguous results. For example, a high percentage of either young or male puma in the harvest may indicate either a source or sink population. Demographic changes in the harvest over successive hunting seasons are needed to clearly identify source or sink status. Finally, although the demographic information may be valuable information as to whether a population is increasing or decreasing, this sort of index is not as desirable for setting management policy as actual population size (Negri & Quigley 2010). Habitat suitability models based on harvest location data are used in conjunction with potential densities to produce population estimates. Habitat suitability models for pumas have been used by the state of New Mexico to estimate state hunt unit puma populations and to set depredation and harvest limits (Negri & Quigley 2010). The puma density estimates used in these models are taken from a few intensive, published studies of puma populations that have been conducted in a variety of locations. Unfortunately, the study locations
may bear little resemblance to the management area to which they are applied. Another potential problem is the geographic bias in harvest data, as hunters may concentrate their efforts in accessible areas with snow, but avoid inaccessible regions (Anderson & Lindzey 2005; Logan & Sweanor 2001). The utility of these models would be greatly enhanced if they could be more easily verified by an accurate, more efficient, and independent assessment of population size. This utility depends on cost effective means of testing predicted puma densities that currently do not exist (Hirzel et al. 2006; Negri & Quigley 2010).

Invasive survey techniques for puma involve the capture and marking or collaring (with telemetry or GPS equipment) of individuals to perform mark-recapture or mark-resight estimates or to allow for direct counts. Because of puma natural history and behavior, direct measurement of puma population density is expensive in time, money, and equipment and is not cost effective over large areas (Beck et al. 2005; Hemker et al. 1984; Laundré et al. 2007; Logan & Sweanor 2001; Ross & Jalkotzy 1992).

The primary non-invasive techniques employed for puma include: surveys for natural sign including tracks, scat, and scrapes, hair sampling, and the use of remote cameras. Track and scat surveys are usually limited to detecting the presence of puma in an area because it is difficult to estimate puma distribution, relative and absolute abundance, and monitor trends in population using just sign, except under very specific conditions (Heinemeyer et al. 2008). Track surveys may provide definitive presence absence data or a general index of population increase or decrease. However, considerable effort may be needed to detect changes in population size. Beier and
Cunningham (1996) found that 140 transects were needed to detect a 30% increase in population size with 80% power at \( \alpha = 0.05 \). However, they also found that track surveys might be the most efficient technique to detect large fluctuations (50%) in population size. If tracks can be identified to individuals, a mark-resight framework may be used to generate actual population estimates (Balme et al. 2009). A significant limitation to the use of track surveys is that they require skilled surveyors and are only possible in areas with an adequate distribution of suitable substrate (Anderson et al. 2010; Heinemeyer et al. 2008; Ray & Zielinski 2008; Smallwood & Fitzhugh 1995; Van Dyke et al. 1986).

Scat surveys are usually performed to determine presence/absence and are often used in conjunction with track surveys, given the relatively lower density and detectability of scats (Heinemeyer et al. 2008). Recently, the use of scat detection dogs has increased the feasibility of scat surveys (MacKay et al. 2008a). Likewise, the use of molecular techniques that allow the identification of individuals from scats has allowed for true population estimates to be generated from scat collection surveys. Ernest et al. (2000) successfully used fecal DNA microsatellites to estimate a minimum mountain lion population size in Yosemite Valley, and Miotto et al. (2007) used sequences from the mitochondrial cytochrome b gene obtained from fecal samples to estimate the puma population in two protected areas in the state of Sao Paulo, Brazil.

Hair sampling may also produce presence/absence data or population estimates based on molecular identification of individuals. Kendal and McKelvey (2008) provide an extensive review of hair collection methods. The use of rubbing pads baited with scents that entice felids to rub against them has been used successfully for bobcats and
lynx. Although puma have been detected at the same rate as lynx by the National Lynx Survey, Beier and Cunningham (1996) found the technique did not detect puma known to be present, and Sawaya et al. (2008) found the technique produced lower than expected detection rates (Kendall & McKelvey 2008). Further, Sawaya et al. (2008) found that backtracking in snow to bedding sites produced more successful hair capture than did rubbing pads.

Remote cameras are a non-invasive survey tool that is rapidly increasing in sophistication, practicality, and utility. The first use of an animal triggered remote camera occurred in 1877 when a galloping horse was photographed by a series of cameras triggered by trip wires. By the turn of the century remote cameras were being used to study nesting birds. The first use of remote cameras in the wildlife literature appeared in the 1950’s when Gysel and Davis (1956) published instructions for a wildlife photographing system (Cutler & Swann 1999). Their use as tools for research and management however was slowed by their size, cost, and time requirements. By the 1980’s, camera cost, size, and reliability had reached the point that their use as a research tool was feasible. By the 1990’s, the use of remote cameras was growing dramatically. In 1997 Cutler and Swann (1999) reviewed 107 peer reviewed wildlife studies that had used remote cameras. Of these 107 studies, 7% had used remote cameras to gather data on population parameters.

Remote cameras are typically used to meet one of three objectives: (1) detecting species presence; (2) estimating population size; and (3) recording behavior. Numerous studies reference the use of remote cameras to detect pumas dating back to Chapman
Remote camera traps have proven to be a useful tool for developing population density estimates using non-invasive mark-resight techniques for individually identifiable felids like tigers (Karanth 1995; Karanth & Nichols 1998; Kawanishi & Sunquist 2004; Linkie et al. 2006; O'Brien et al. 2003), jaguars (Espinoza et al. 2003; Kelly 2003; Maffei et al. 2004; McCain & Childs 2008; Silver et al. 2004), bobcats (Heilbrun et al. 2006; Symmank et al. 2008), ocelots (Bitetti et al. 2006; Dillon & Kelly 2007; Maffei et al. 2005; Trolle & Kery 2003), and Geoffroy’s cats (Cuellar et al. 2006). Pumas, however, are not easily individually identified in photos because they have no definite characteristic markings, making mark-resight analysis difficult. Kelly et al. (2008) produced a major advance in puma management by demonstrating that population mark re-sight estimate of unmarked pumas using remote cameras was possible. Unfortunately, there are a number of peculiarities this technique requires that may make it unfeasible in many situations. For example, expert puma biologists are needed to indentify individual pumas in photos. In addition, the technique “…is tedious work requiring extreme attention to detail that only some investigators possess.” Further, Kelly et al. (2008) suggest that 2 to 3 investigators conduct blind identification and then compare results to identify and potentially resolve discrepancies. Because pumas are not good candidates for noninvasive mark-resight studies, the development of remote camera population estimates for puma should focus on techniques that do not require individuals to be identified. Although a wide variety of
techniques can be used with varying success to detect pumas, and at least in the case of
the techniques developed by Kelly et al. (2008), be used to estimate puma population
density, current methods for estimating puma population density are largely impractical
over large areas and in many contexts, because of either the need for particular expertise,
specific conditions (such as substrate), or the cost and effort required for an estimate
(capture and marking) that is not readily extrapolated to other puma populations
(Anderson et al. 2010; Beck et al. 2005; Smallwood 1997).

As a result, throughout the puma’s (Puma concolor) extensive range, population
estimates are either not available, as in most of Central and South America (Kelly et al.
2008; Laundre & Hernandez 2010), or are limited in range or accuracy, as in the western
United States (Logan & Sweanor 2001). Because of inherent difficulties in estimating
puma population density, a technique for accurately and efficiently measuring and
monitoring puma populations is needed to further explore puma ecology, direct puma
management, and guide puma conservation efforts (Beck et al. 2005).

Due to a lack of puma population data, wildlife managers in the western U.S.
struggle with balancing traditional management concerns like sport hunting and
depredation with growing conservation interest in pumas (Beck et al. 2005). Data on
puma populations are especially needed where wildlife conservation goals conflict over
puma management, as when puma predation threatens endangered species like the desert
bighorn sheep (Ovis canadensis nelsoni) (Clemenza et al. 2009; Rominger et al. 2004).
A technique to efficiently determine puma densities would help define ecological
relationships between puma and prey densities, and give managers a tool for linking
puma population levels with puma impact on vulnerable species, large game, and livestock (Beck et al. 2005; Logan & Sweanor 2001; Ruth & Murphy 2010). Such a tool would also allow for easier testing of predictions about puma and prey interactions and relative densities that have not been addressed in most of the puma’s range (Karanth & Nichols 1998).

Given the pressing need for accurate puma population density estimates throughout the species range as well as a cost-effective technique for generating those estimates, we were inspired by Carbone et al.’s (2001) demonstration that the frequency of photo capture in tiger populations was correlated with mark-resight population estimates, suggesting that photo frequency itself may be used to estimate populations of animals that are not naturally individually identifiable. Recognizing the potential application of Carbone et al.’s (2001) work, the primary objective of our study was to develop a cost effective management tool for estimating unmarked puma populations with a quantifiable degree of certainty using only a standardized remote camera array. Our goal was to use either a known population or a mark-resight population estimate to calibrate the relationship between photo frequency and estimated population size for puma. Carbone et al. (2001) also used a model of tiger movement to estimate the minimum camera effort required to detect tiger presence. Similarly, our second objective was to empirically measure the mean camera effort needed to detect the presence of resident adult pumas with 95% certainty. Finally, we examined the effect of camera density on probability of puma detection.
METHODS

STUDY AREA

This study was conducted on a 100 km² portion of the 1134 km² Ladder Ranch on the eastern slope of the Black Range, in the Aldo Leopold Wilderness of the Gila National Forest, Sierra Country, New Mexico. Elevation on the ranch ranges from 1,340 m to 3,099 m above sea level along the Black Range continental divide and covers a diversity of habitat types including Chihuahuan desert scrub, desert grassland (ecotone), coniferous and mixed woodland, subalpine coniferous forest, montane coniferous forest, farmland and open water (New Mexico Resource Geographic Information System program, University of New Mexico). Four perennial streams flow through the ranch including North Palomas Creek, South Palomas Creek, Seco Creek, and Animas Creek. The latter two flow through the camera grid sampling area. Pumas are hunted as a big game species in New Mexico, and hunting occurs on public land leased by the ranch in areas near and bordering the camera study area. The Ladder Ranch is a working bison ranch that also hosts elk, mule deer, wild turkey, javelina, and puma hunts.

FIELD WORK

Five individually GPS-collared pumas were followed over the course of the study: 3 GPS collared females and 2 GPS collared males. Pumas were captured using leg hold snares (Logan et al. 1999) or with hounds. Pumas were tranquilized with Ketamed (2mg/kg ketamine plus 0.075 mg/kg medetomidine) and given the antagonist atipamezole.
(Antesedan®) as suggested by (Kreeger 1999). Captured pumas were fitted with unique ear tags and either a Telonics MOD-500 VHF transmitter collar (265g), a Telonics TGW-4480 Argos GPS collar (425-700g) or a Northstar NSG-D1 Globalstar GPS collar (725-1005g), depending on availability.

As suggested by Karanth et al. (2002), our original camera array was arranged in a 4x4 cell grid with 16 single cameras placed one in each 4 km$^2$ grid cell. This camera array ran from May 18, 2008 to February 20, 2010 in an area on the ranch with historically high puma densities (Orvel Fletcher, pers. comm.). The array was expanded to 25 single cameras in a 5x5 grid covering a 100 km$^2$ area on November 11, 2009. We collected photo data with this array until January 20, 2010. Cuddeback Expert 3.0 megapixel Flash Cameras were used because they represented most appropriate balance between cost and quality for this study. Individual cameras were placed within grid cells in the location that was determined to have the highest probability of detecting puma movement (Karanth et al. 2002). Camera locations were chosen after scouting for sign, reviewing topographic maps of the area, and consulting puma biologists and hunters with local knowledge of the area (Figure 2.1). Camera locations included riparian game trails, ridgeline game trails, and dry washes. Due to flash flooding, cameras were usually anchored to trees or large shrubs at a variety of heights, and aimed diagonally across the suspected travel path to detect movement around an average puma shoulder height of approximately 50 cm. Cameras were checked once per month, on average, to download images, change batteries, reset location in the event of movement, and deal with malfunctioning cameras.
DATA MANAGEMENT

Camera running days were defined as any day when the camera ran continuously from 1200 h one day to 1200 h the following day, and these were recorded for all cameras throughout the course of the study. Individual camera capture histories were built for each marked puma based on records of camera running days and photo captures across all 25 cameras. The status and capture success of each camera was recorded for every day of the survey by looking through photos to determine the camera’s running history and capture success for all survey days. Daily probabilities of detection for each of the cameras for all marked pumas were calculated from these capture histories. Puma GPS locations were mapped weekly to monitor puma movements within the camera grid. A photo database and online archive for all photos was maintained and incorporated all photos taken by grid cameras during the survey. All images were catalogued and data recording the date, time, and species captured for each image were incorporated into the database.

DATA ANALYSIS

Data analysis was accomplished in eight stages: (1) a nightly photo capture history matrix was assembled by individual camera for each puma, where zeros indicated a night when no puma photo was taken and a one indicated a photo capture; (2) for each puma this photo capture history was then modified by mapping nightly movements to determine whether a puma was within range of a camera on any given night. Zeros in the
matrix for nights when a puma was not within range a particular camera were changed to null values; (3) for each puma, the capture history was further modified by changing zeros to null values for any night that a particular camera was not operating; (4) using this modified photo capture history, post-hoc detection probabilities were smoothed across all cameras; (5) the resulting 25 smoothed camera detection probabilities were then sampled in all combinations of each number of cameras from 1 to 25 cameras; (6) the mean number of camera nights to reach 95% probability of puma detection and the probability of detection were calculated for all of the sampled combinations to examine the functions by which puma detection varies with camera number and camera density; (7) the 95% probability of detection was used with the number of puma detections to estimate the puma population, and finally; (8) the population estimate derived from the 95% detection probability was compared to a common mark-resight population estimate.

Nightly photo capture histories were modified by puma movement data in the following manner (Figure 2.2): For each night (1800 h - 0900 h) that we had at least five GPS locations for a puma, we calculated kernel density estimates of each individual's 95% home range contour, using the package adehabitat (Calenge 2006) in R (v.2.7.2). The functions kernelUD and getverticeshr implement Worton's (1995) approach to estimating the utilization distribution, a bivariate probability density function that defines the minimum area in which an individual has a user-specified probability of being located (Calenge 2006). We used the default, ad hoc method for determining the bandwidth (h) for the kernel density estimates, which assumes a bivariate normal distribution, because (1) the least-squares cross-validation method failed to converge for many nights of data
and is more prone to fail when points are tightly clustered in space (Gitzen et al. 2006), such as when a puma is on a kill, and (2) the resulting bandwidths approximated those manually determined for a subset of nights to yield the smallest yet contiguous home range. After converting the home range contour to class gpc.poly using the package gpclib, we then used the function inside.owin from the package spatstat to determine which cameras fell inside each of the nightly home ranges for each individual. This allowed us to determine when an individual was in range of a camera but was not captured. Capture histories were then modified to reflect when cameras were available to capture marked puma movement within the grid.

To smooth detection probabilities and calculate how 95% detection probability varied with camera number, camera density, and individual puma we used SAS software (Version 9.2 of the SAS System for Windows © 2007). Proc glimmix was used to smooth daily capture probabilities across all cameras with radial smoothing. The resulting 25 smoothed daily probabilities of detection, one for each camera in the array, were sampled to estimate the mean number of camera running days to reach 95% probability of puma detection. To determine the camera density that maximized puma detection probability, mean inter-camera cell distances were also calculated for all sampled combinations of cameras and probability of detection was calculated and graphed with mean inter-camera cell distance for all number of cameras 2-25. A linear trend line was fit to the mean inter-camera cell distance versus puma detection probability graphs to examine the affect on probability of puma detection of decreasing the camera density for all number of cameras 2-25. To generate the mean number of
camera nights required to detect LF1 with 95% certainty, we ran the above analysis for her based on 26 photos of her captured over 8,044 total camera nights of the 16-camera array running for 6,859 total camera nights and 562 calendar days from April 28, 2008 to November 10, 2009, and the 25-camera array running for 1,188 total camera nights and 71 calendar days from November 11, 2009 to January 20, 2010. LM3’s analysis was based on 9 photos of him captured over 1,309 total camera nights of the 16-camera array running for 121 total camera nights and 10 calendar days from November 1, 2009 to November 10, 2009, and the 25-camera array running for 1,188 total camera nights and 71 calendar days from November 11, 2009 to January 20, 2010.

Both population estimates were based on 1,188 total camera nights of the full 25-camera array running for 71 calendar days from November 11, 2009 to January 20, 2010. During the survey we captured 32 adult puma photos. A standard mark-resight population estimate was calculated using the program NOREMARK, an immigration-emigration mark-resight model, and 5 individually GPS collared pumas (White 1996). Density was determined by dividing the population estimate by an effective area equal to the total area of the 100 km² camera grid and a buffer estimated to be the radius of a puma’s home range. The radius of a puma’s home range was estimated using 2 different methods: using marked puma photo data to estimate half of mean maximum distance moved (MMDM)(Nichols & Karanth 2002) and using puma GPS movement data to estimate half of MMDM (Soisalo & Cavalcanti 2006). The resulting population density estimates were compared. A population estimate based only on photo capture rate (Carbone et al. 2001) was calculated using all puma photos and the following equation:
The mean number of camera nights to reach 95% probability of detection comes from our first analysis, and depends on how many cameras are in your camera array. For our estimate we averaged the mean number of camera nights required to detect LF1 (60.134084 camera nights) and LM3 (74.77443775 camera nights) with 95% certainty using a 25-camera array as the value for mean camera nights to reach 95% capture probability (67.45426088 camera nights). Our rate of capture population estimate was generated from 32 observed puma photos captured during a survey including all 25 cameras running. The population estimates produced by the two different models were compared to determine the practicality of using puma photo capture rates to estimate puma population size.
RESULTS

CAMERA EFFORT FOR 95% DETECTION PROBABILITY

The number of camera nights required for 95% probability of detection decreases as a negative power function for both study animals as the number of cameras is increased. At low camera numbers the number of camera nights required for 95% probability of detection is dramatically greater for the male than the female. However, this difference in the camera effort required for 95% detection probability between the two study animals decreases markedly as the number of cameras increases (Figure 3.1). For all numbers of cameras, it requires fewer trap nights to detect LF1 than it does to detect LM3. The mean number of camera nights required for 95% detection probability for LM3 varied between 5,127 camera nights for one camera to 74 camera nights for 25 cameras, as a negative power function described as $Y = 1,393.9X^{-1.042}$, $R^2 = 0.82$, $p < 0.01$ (Figure 3.2). The mean number of camera nights required for 95% detection probability for LF1 varied between 74 camera nights for one camera and 60 camera nights for 25 cameras, as a negative power function described as $Y = 69.243X^{-0.05}$, $R^2 = 0.82$, $p < 0.01$. Because the data sets of sampled camera probability combinations were all generated from the same 25 cameras, the data points are not independent, and, as a result, the above functions are only an initial description of the data meant to roughly characterize the relationship between the variables. The p-values are not representative of these functions adequately describing the data and also do not represent the result of an exhaustive effort to fit a model to the data because the assumption of independence has not been met.
CAMERA ARRANGEMENT

The probability of detection, for one running night with the sampled array, increased slightly as mean inter-camera distance for a set number of cameras was increased. This slight positive trend between inter-camera distance or camera density and probability of detection was observed for all cameras > 1 for both LF1 and LM3 (Figure 3.4). Spreading cameras out, or decreasing the density of the camera array, yielded a higher probability of detection.

DENSITY ESTIMATE

Population density estimates are presented in Table 3.1. Our rate of encounter population density estimate of 1.8 (1.4 – 2.2) pumas/100 km$^2$ was calculated using the camera array study area as the effective area (100 km$^2$). This population estimate fell within the 95% confidence interval of the mark-resight daily population estimate of 2.1 (1.7-4.4) pumas/100 km$^2$, calculated with 3 different effective areas including the camera array study area (100 km$^2$), the camera data generated MMDM (188 km$^2$) and a GPS data generated MMDM (1,087 km$^2$) as an effective area.
DISCUSSION

With a remote camera array and individually GPS collared pumas, we were able to determine the mean number of camera nights needed to detect a single resident puma’s presence with 95% certainty. Using our calculated probability of puma detection we were able to develop a technique to estimate population densities of unmarked resident pumas based on photo capture frequency. Unlike other remote camera survey techniques, the method we have developed uses an array of single camera sets, does not require individual identification of animals, and considers the effect of number and density of cameras used in a survey grid.

Although we found an expected negative relationship between the number of cameras included in the survey and the mean number of camera nights needed to detect a puma, the relationship was not linear (Figure 3.1). Initial increases in the number of cameras used resulted in large gains in puma detection, but as more cameras are added the function begins to reach an asymptote where adding more cameras inside our 100 km² study area does not appreciably decrease the number of camera nights needed to detect a puma. When the asymptote has been reached, the associated number of cameras can be interpreted as an estimate of the most effective number of cameras for surveying puma presence in the study area. Accordingly, our camera array design seems to fit our study area and species of interest because at 25 cameras the mean number of camera nights to detect a male and female puma has reached an asymptote. Along with recommending how many camera nights an array needs to be running to detect the presence of a puma, depending on how many cameras are in the array, the relationship between number of
cameras and number of camera nights needed to detect a puma can also be used to determine the most effective number of cameras to use in a puma density survey.

The total number of individual camera nights needed to detect the presence of a male (75 camera nights) or female (65 camera nights) puma added up to a 25 camera array running for 3 consecutive nights to detect the presence of a resident puma of either sex. The difference we found between the number of camera nights needed to detect the male versus the female may at this point be an artifact of low sample size. A variable that may have affected the rate of photo captures for the female during the sampling period was her reproductive status. During the sampling period from April 28, 2008 to January 20, 2010 LF1 was known to have 2 separate litters both with den sites in the Animas Creek drainage. The first litter, born around August 7, 2008, was comprised of 2 kittens, that we could confirm, and the den site was located 6.05 km from the camera array. During denning and caring for this first litter of kittens from August 7, 2008 to around September 12, 2009 LF1’s rate of photo capture was 1.9 photos per 1000 camera nights. The second litter, born around September 12, 2009, was comprised of 3 kittens, and the den site was located inside the camera array. During denning and caring for the second litter from around September 12, 2009 to January 20, 2010 LF1’s rate of photo capture was 5.4 photos per 1000 camera nights. While LF1 was caring for her second litter her GPS movements remained almost entirely within the camera array and were localized around her den site. Her travel pathways to and from the den site to kill sites in the area during this time frequently brought her within capture range of several of our grid cameras. LF1’s den site’s relative location to the camera array most likely
contributed to the difference in rate of capture between these two time periods. During the period of time we were sampling before her first confirmed litter of kittens from April 28, 2008 to August 7, 2008 her rate of capture was 5.7 photos per 1000 camera nights. This photo capture rate observed for LF1 during a period of unknown reproductive status is comparable to the one observed after her second litter and may suggest that during that time she was caring for a litter whose den site was located within the camera array.

Based on our data it would appear a female’s reproductive status and the location of her den in relation to the camera array may be major factors in determining the probability of photo capture for a resident female and should be considered when estimating population density with photo capture frequencies. More data is needed on female puma movements and photo capture frequency during different reproductive stages to provide an average of female photo capture frequency and allow for the further development of our rate of capture population density estimating technique. With long term camera array monitoring Karanth et al. (2006) were able to estimate tiger population dynamics including tiger abundance, density, annual survival rates, number of new recruits, and rate of population change over time. With more study the detectable differences in photo capture rate depending on reproductive condition may provide a way to estimate female reproductive status of individually identifiable females based on their photo capture rate during long-term camera monitoring.

Beyond considerations of the potential variability of female photo capture frequency, another explanation for higher rates of female photo capture compared to a male may be the relative size of their home ranges. Female pumas are geared toward
raising offspring, and as a result they have smaller home ranges, in North America from 55 km$^2$ to over 300 km$^2$, and less extensive daily movements than adult male pumas (Logan & Sweanor 2001; Sweanor 1990; Sweanor et al. 2004). Male pumas have on average one-half to three times greater territory sizes, ranging in North America from 150 km$^2$ up to 700 km$^2$ (Logan & Sweanor 2000, 2001), and more extensive daily movements than females as a result of their drive to seek out prospective mates and competitors (Logan & Sweanor 2001; Sweanor 1990; Sweanor et al. 2004). The average home ranges of LF1 and LM3 over the course of the study were 83 km$^2$ and 383 km$^2$ respectively. While males are known to travel greater distances per night than females (Logan & Sweanor 2001; Sweanor 1990), with large home ranges that are not likely to be entirely encompassed by a camera array, it is expected that a male would pass through the same areas with a longer periodicity than a female resulting in a lower rate of photo capture for males. Again, more photo capture data from camera arrays is needed on pumas across different habitat types to generate an average photo capture rate for males and females, and allow for the fine-tuning of our rate of capture population estimate.

Along with choosing an appropriate number of cameras for a survey, the area covered and the density of cameras should be designed to maximize probability of detection while also making the most efficient use of a limited number of cameras (Kays & Slauson 2008). Our analysis to determine the best camera design for detecting puma with 95% certainty suggests that the number of cameras within a camera array affects detection probability more than camera spread and that the most effective number and density of cameras, based on a set survey area, is determined by the asymptotic
relationship between the number of cameras used in the survey and the mean number of camera nights to detect a puma. The design of a sampling area for a camera array survey should be informed by the home range size of the target species (Kays & Slauson 2008; Long & Zielinski 2008) and the average distance traveled by the target species in one activity period (Karanth et al. 2002). Once the appropriate study area size and number of cameras for the study area is chosen, designing the camera array to maximize camera spread within the study area should also maximize detection probability for that number of cameras. Increasing distance between cameras within a set study area may continue to increase probability of capture (Figure 3.4), but distance between cameras and density of cameras must also be designed to decrease the chance of missing photo captures of animals because they are regularly able to move between the cameras and not get captured (Kays & Slauson 2008; Long & Zielinski 2008). Because our puma home ranges and nightly movement were comparable to tigers surveyed by Karanth et al. (2002) we also chose to set cameras in 2 km² grid sections arranged in a square to cover an area roughly the average size of a female puma’s home range. If resources do not allow for the most effective number of cameras to be used, puma detection and estimation of population density can still be accomplish with the compromise of increasing the number of camera nights needed to survey puma presence with 95% certainty. An advantage of our method of estimating population density using rate of capture and a single camera per grid section is that probability of detection can be increased and survey time to estimate population density in an area decreased because extra cameras can be used to increase density and survey area covered instead of being
paired with other cameras in the same grid section for the purpose of identifying individuals of the species.

Another advantage of using single cameras and being able to increase the number of grid cells in a camera survey is the ability to sample a diversity of local features like game trails, ridge lines, riparian corridors, etc. (Kays & Slauson 2008). Across our camera array and study area the probability of detection varied across individual cameras and the larger differences were most likely the result of these differences in local features and differences in the rate pumas choose to travel through these local areas. While we corrected for the large differences in probability of detection across local features and cameras using radial smoothing, the different rates of detection relative to local features could give researchers a clearer picture of how pumas use the landscape. Cameras located along game trails in riparian corridors captured the greatest number of puma photos and maintained the highest rates of puma photo capture throughout our sampling. Cameras set along dry washes, the most common local feature for camera sets, had a wide range of capture probabilities. Some of these cameras at times had puma photo capture rates comparable to riparian corridor cameras and others never captured a puma photo. More detailed descriptions or surveys of local camera sites in dry washes may help to elucidate the differences between these sites and better predict puma travel pathways. In the future a method for obtaining more detailed descriptions of camera locations across one or many study sites may help predict and recommend better and better camera locations for detecting pumas on common travel pathways across a wide range of habitats they occupy.
Rates of detection for a species will vary not only across camera locations within one camera array, but perhaps more so across different terrain among field sites across the range of the species. The puma once had the broadest geographic distribution of any terrestrial mammal in the Western Hemisphere other than humans (Young 1946). Even though its range has declined there are vast differences in habitat types that pumas occupy across their range. From the Florida Everglades to the mountains of Patagonia, puma management and conservation need to be guided by accurate and efficient population estimates. For tigers, a species that also maintains a large geographical range extending across a variety of habitats in Asia, Carbone et al. (2001) found that estimates of average photographic rates for tigers across study sites distributed throughout their range could provide a robust measure of tiger density because the relationship between rate of photo capture and number of individuals holds despite local and regional variation. The differences between habitat types where pumas range are vast and provide unique challenges to developing methodologies and study designs that are effective and efficient across many different habitat types. Based on the findings of Carbone et al. (2001) we hope that future expansion of our analysis to incorporate averaging rates of capture across a variety of study sites distributed throughout the geographical range for pumas will allow for the further development of this technique to provide a robust measure of puma densities across all habitats where pumas occur.

Our rate of photo capture method may provide a more efficient and accurate means of detecting puma presence and estimating puma population densities when compared to more traditional methods like mark-resight surveys for pumas, but a
limitation of the method is the inability to distinguish between resident and dispersing animals because individuals are not identified. In terms of estimating how many camera nights are required to detect a puma with 95% certainty our analysis was based only on detection rates for GPS collared resident pumas. Therefore the length of sampling for camera array surveys to determine puma presence in an area should be designed to be of long enough duration that it is able to detect the difference between an area that has only dispersing pumas occasionally passing through and an area that has a resident population of pumas. Dispersing pumas are most likely males who would pass through the camera array for a limited amount of time and as a result have a low probability of photo capture relative to the resident pumas in the area. We recognize this potential source of error, but since transient animals have near-zero probability of being recaptured at a later time (Karanth et al. 2006; Pradel et al. 1997) we expect that the occasional photo capture of a dispersing animal would not contribute to an appreciable difference in estimating puma population density.

The accepted method of calculating animal density based on a camera array mark re-sight population estimates (Nichols & Karanth 2002), has been standardized across many different camera array studies (Carbone et al. 2001; Karanth & Nichols 1998; Kelly et al. 2008) and relies on an estimate of the effective area surveyed. The buffer determining the effective area used to calculate density with this method has traditionally been estimated by camera movement data to be the radius of a home range based on half of the mean maximum distance moved (MMDM) determined by camera information alone (area = 188 km$^2$). Based on a MMDM calculated from puma GPS movement data
using the camera information alone seems to represent a gross underestimation compared to the GPS driven estimate of effective area (area = 1087 km$^2$). Our results suggest that using half of MMDM estimated with camera data would overestimate puma population density, and Soisalo and Cavalcanti (2006) found that distance moved and minimum home ranges estimated from relatively short camera array data sets were highly unrepresentative of true movement distances and home range size for jaguars. However, Balme et al. (2009) found that this traditional method did not grossly overestimate population density and was the next best estimator after a new technique where the mean maximum distance moved outside the survey area (MMDMOSA), determined by telemetry, was used to estimate the buffer and the effective area. It is likely that MMDMOSA calculated using GPS data would be even more accurate at estimating effective area and population density, but we have not yet conducted this newly suggested analysis and so have relied on the half camera grid estimated MMDM effective area estimate for our mark-resight comparative population density estimate. Because we did not identify individuals for our rate of photo capture puma density estimate a MMDM based on identifying maximum distances moved by individuals could not be calculated and as a result we based our model on the designed survey area covered by the camera array (area = 100 km$^2$). Using the exact area of the camera grid as the effective area we were able to generate a puma density estimate comparable to the daily mark-resight density estimate. Although more data and comparisons across different study sites is needed to further corroborate this technique of estimating effective area for our rate of
photo capture density estimate, our initial success suggests it may be an effective means of estimating effective area for our density model.

To adequately develop and assess the effectiveness of a puma population density estimator it must be compared to independent estimates of animal density at representative sites across the geographic range of the puma in order to calibrate the photographic rates (Carbone et al. 2001). We compared our rate of photo capture population density estimate to a mark-resight population density estimate considered to be the gold standard in abundance estimation for animals that can be individually identified which we achieved by capturing and marking pumas with GPS collars and ear tags (Nichols & Dickman 1996). To further refine our estimate and develop this technique we need to incorporate standardized camera arrays at study sites where independent population estimates are being conducted. By standardizing camera arrays, data collection, and management techniques camera data from many different studies could contribute to the development of new techniques that benefit the study animals (Kays & Slauson 2008). Ideally future studies will pair long-term intensive monitoring of a puma population through traditional mark-recapture techniques with a long running camera array in the same area providing the best opportunity for calibrating photographic rates, comparing instantaneous population density estimates, and comparing how the two methods monitor changing abundance levels over time.

Unlike similar studies that have addressed the question of how many camera nights it requires to detect individual species with a specified level of certainty (Carbone et al. 2001; Tobler et al. 2008), we also considered the affect of how many cameras those
camera nights were spread across in calculating our minimum detection requirements.

By calculating camera effort required to detect resident pumas by number of cameras we were able to incorporate the number of cameras used for a camera array survey into our model for estimating puma population density. While increasing the number of cameras and the area covered by a camera grid confers a higher detection probability and a shorter sampling period to achieve detection of puma presence and puma abundance there are practical limitations to funding and monitoring a large camera array. Our rate of photo capture population density estimate was designed to be flexible in terms of the number of cameras needed to perform an efficient survey of puma abundance in an area. This consideration allows our survey method to cater to the specific needs of monitoring projects’ different size budgets and survey areas. The trade off for having fewer cameras to contribute to an array is the longer running time needed for the array to adequately estimate puma presence or abundance. The added survey time may be well worth the decreased cost for some applications of this survey method.

Another consideration for developing a technique for estimating puma population density based on rate of photo capture is the observed difference between the rate of photo capture for males and females (Figure 3.1). If most photographed pumas could accurately be assigned a sex then we could incorporate a ratio of male, female, and unknown puma photos into our population model, but this is not the case. Our non-baited single trail camera sets do not regularly produce puma photos that can be definitely identified to sex. Because of this we averaged LF1 and LM3’s mean number of camera
days to reach 95% probability of detection for calculating the population density estimate and we did not consider sex when counting puma photos.

Dispersing individuals have the potential to decrease the accuracy of puma population estimates whether using a mark-resight model or our probability of detection approach. Transient pumas may be detected by a camera array but, as they are by definition spending little time in given area, it is unlikely. Increasing camera number should decrease the number of transients photographed, as the array would be in operation for a shorter period of time, and thereby reduce the opportunity for transients to be detected.

A primary issue in puma management and conservation today is the current distribution of pumas within the continental U.S. and their expansion into areas from which they were previously extirpated (Anderson et al. 2010; Gill 2010). The Florida panther is perhaps the best example of a puma population that is being intensively monitored because its ability to endure as a small population is uncertain despite great management efforts. Long-term hopes for the isolated population depend on its potential for expanding out into surrounding areas where pumas have been extirpated since the beginning of the twentieth century (Nowak 1976). Given these conditions the Florida panthers could serve as an excellent case study to further develop camera array techniques that could help monitor fluctuations in the population over time using non-invasive means. Further, the Florida panther recovery area could serve as a test case to evaluate the impact of habitat type on detection probability. This comparison would add to the utility of this technique for the Eastern puma. The potential for Florida panthers to
disperse into surrounding areas into the former distribution of the Eastern puma brings up the difficulty of accurately being able to measure in a quantifiable way if a species is present in an area, or perhaps more difficult, absent from an area.

The status of the Eastern puma is controversial, but there remains no definitive scientific evidence that there are any remaining or re-established populations of resident pumas living in their former eastern range outside of the Florida population (Lotz 2005). The controversy surrounding the Eastern puma is largely the result of an inability to efficiently survey the presence or absence of resident pumas. Our probability of detection survey method was designed partially to meet the specific need of detecting even a single resident animal and can therefore serve as a quantifiable measure of presence or absence for an area.

The Midwest is another area where there is a need for a cost-effective means of detecting the establishment of new puma populations. Although the presence of resident puma populations east of the Dakotas has not been confirmed, what is clear is that puma are dispersing into the mid-western states. There are a number of incidents where puma have been confirmed in Nebraska, Kansas, Oklahoma, Minnesota, Illinois, Wisconsin, Michigan, Iowa, Missouri, and Arkansas (Anderson et al. 2010). While it is uncertain whether many of these animals were the result of captive releases, it is known that wild, radio-collared puma have dispersed long distances from South Dakota to Minnesota and Oklahoma. The notion that pumas dispersing from Rocky Mountain states might be able to recolonize former habitats to the east has been confirmed by the re-establishment of puma populations in North Dakota, South Dakota, and Nebraska in the last few decades.
(Anderson et al. 2010.) Using what we have learned from the New Mexico study, the use of remote camera arrays should allow for the quantification of presence or absence of puma in areas where they may be suspected to have recolonized.

The use of our detection probability technique for detecting either a single resident puma with quantifiable certainty or estimating puma population size lends itself to productive use in an adaptive management context. An important aspect of that adaptive management approach is that management policies are stated as testable hypotheses. This allows for testing predictions about species population sizes and distributions as well as the impact of management decisions on those populations.

Camera arrays capable of quantifiably detecting puma presence or estimating puma population sizes have great potential for informing adaptive puma management. The use of habitat suitability models that predict puma density across a region, and therefore puma population size, would achieve their greatest utility if used as predictive hypotheses that could be cost-effectively tested and refined. Our probability of detection technique could be used as a cost-effective means to test the model’s predicted puma population densities across a representative sample of habitat suitability types. A similar approach may be used to facilitate early detection of newly established puma populations in Florida, the eastern U.S. or the Mid-west. Habitat suitability models could provide predictions as to where puma are likely to reestablish. Remote camera arrays could be deployed and monitored long-term in the areas most likely to be colonized and serve to alert managers of puma colonization with a degree of quantifiable confidence.
In summary, our study demonstrates that there is a quantifiable relationship between puma photo capture and puma population size, making the use of remote camera arrays with unmarked puma populations a cost-effective means of estimating puma populations. The results of our probability of detection method agree with traditional mark-resight population estimates at a fraction of the cost. The technique needs to be refined further with the use of additional pumas of both sexes to calculate a more representative mean detection probability. Also, the technique needs to be repeated across a variety of habitat types to determine the extent to which this method can be used in other contexts. As suggested by Jennelle et al. (2002), we encourage other puma researchers, who may already have marked study animals, to consider establishing standardized remote camera arrays, as discussed here, in order to further explore the potential of this technique for widespread use.
MANAGEMENT IMPLICATIONS

In the course of our study we ran a remote camera array of 16 to 25 cameras continuously from 18 May, 2008 to 20 January, 2010 producing over 18,000 catalogued and archived photos (summarized by mammal species in Figure C.1). The operation of this camera array and the data it generated has provided us with unique insight into the management implications and applications of remote camera arrays, particularly in the southwest.

Adaptive management is a management protocol that utilizes the constant input of information to refine policies and practices (Holling 1978). Policies and procedures are posed not as rigid mandates but essentially as testable hypotheses. An integral part of an adaptive management design then is monitoring to provide the constant input of information necessary for testing the efficacy of policy and procedure. Remote cameras are ideally suited to use as monitoring tools in an adaptive management context as they are capable of collecting archival data over long periods of time at a relatively low cost. Most of the cameras in our array have been operating continuously for 27 months at the time of this writing. The primary costs over that time period were the purchase cost of the camera $300, plus a 1 gigabyte flash card $35, and 27 changes of 4 D cell batteries at $4 per change or $108, for a total of $443. Cameras are checked approximately once every two weeks, for 54 total data downloads and battery replacements. In our arrays, 16 cameras could be checked in one 8 hour workday, or one camera per half hour. If we assume a labor pay rate of $15/hour for a field technician, the total cost of camera check time would be $7 camera for 54 checks for a total of $378. The total cost of 27 months
of continuous photographic monitoring of wildlife per camera for our study was then $821 or approximately $1/day. It would be difficult to imagine a lower cost wildlife-monitoring tool that produces comparable, high quality data.

A recent case study illustrates in detail the potential benefits of using remote camera arrays for population estimates for species other than puma. Perry et al. (2010 in press) demonstrated that remote camera arrays were a cost-effective alternative to direct counts using aerial surveys and ground crews for estimating desert bighorn (*Ovis canadensis mexicana*) populations in south central New Mexico. Specifically, Perry et al. (2010 in press) report that in 2008 the cost of their remote-camera survey was $3,412, including six cameras, digital flash cards, batteries, and 12 days of labor (including deployment of cameras, downloading photographs, recording and analyzing data) by a biologist at $100/day. They compared this to ca. $7,000 for a survey using direct observations of the same population. This estimate was derived as follows. In 2008, the desert bighorn aerial survey used a helicopter that cost ca. $5,000, including 1.5 h of ferrying time and 3.5 h of surveying time at $4,700 plus $300 salary for the biologist. The New Mexico Department of Game and Fish conducts surveys on the ground in conjunction with surveys using helicopters for complete counts. Typically, ground surveys involve four biologists paid for 1 day of travel and survey at $250 each/day for a total of $2,000. The total cost of the aerial and ground survey then is about twice the cost of the survey using cameras (Perry et al. 2010 in press).

In addition to cost, the camera array technique had other benefits for the bighorn work. For example, using remote cameras significantly reduced stress and disturbance
from helicopters. Also data from remote cameras could be reviewed at leisure to more accurately assign sex, age, and condition. Finally, the training, experience, and quantity of personnel, and safety risks required to monitor the camera arrays and collect data from photographs was minimal relative to that required for aerial or ground-based surveys.

Moreover, the low cost of remote cameras as a monitoring tool for a diversity of species is further enhanced by the ability to use cameras to monitor multiple species simultaneously, to assess habitat preferences, and to detect predation behavior, reviewed in Cutler and Swann (1999). For example, our cameras have recorded at least 23 species of mammal (Figure C.1), with the possibility of more if more than one species of squirrel and one species of bat was detected. This unique feature of the remote camera as a wildlife-monitoring tool may allow for monitoring costs to be divided among several management or research projects simultaneously. For instance, biologists studying the distribution and habitat associations of rare skunks in south central New Mexico have used data from our camera array. In the course of our puma study we have documented four sympatric species of skunk, striped (*Mephitis mephitis*), hooded (*Mephitis macroura*), hog-nosed (*Conepatus mesoleucus*), and spotted (*Spilogale putorius*). Our camera array provided the first record of hog-nosed skunks east of the continental divide in New Mexico since the early part of the 20th century (Chris Haas, University of New Mexico, pers. comm.). A second research team, working on white-nosed coati (*Nasua nasua*) also used our photo data to refine the geographic distribution of the species in New Mexico. Four photographs of the species from our camera array represent some of
the northern and easternmost records from the U.S. (Dr. Jennifer Frey, New Mexico State University, pers. comm.)

As discussed above, standardized remote camera arrays can also be used to answer questions regarding habitat associations. Camera locations in our array encompassed a variety of habitat types, including desert scrub (creosote and mesquite), desert grassland, juniper grassland, pinyon-juniper woodland, and riparian forest. Our camera data demonstrated striking patterns in species associations with habitat type. For example, a preponderance of coyote (*Canis latrans*), cottontail (*Sylvilagus auduboni*), jackrabbit (*Lepus californicus*), and spotted skunk photographs were recorded in desert shrub whereas the majority of puma, hog-nosed skunk, and javelina (*Peccary tayassu*) were recorded in riparian forest habitats. While it is well known that there are species-specific habitat preferences, remote cameras enable the quantification of those preferences in a detailed and site-specific manner. They may also document avoidance of habitat types, as well as seasonal differences in habitat preference. For example, out of 18,000+ photographs recorded in our study, we have no photographic record of coyote, thought to be an extreme habitat generalist, in riparian forest habitat. We also found that the frequency of elk (*Cervus elaphus*) photographs in riparian forest increased in the fall, possibly indicating a seasonal elevation shift in home range in this elk population.

Mesocarnivores, like large carnivores, present additional challenges to biologists attempting to characterize their populations and habitat preferences. Remote camera arrays may offer a cost-effective means of assessing these species as well, as our work indicates. In our study, we recorded approximately 2,000 mesocarnivore photos,
including gray fox (*Urocyon cinereoargenteus*), bobcat (*Lynx rufus*), coyote, striped skunk, hooded skunk, hog-nosed skunk, spotted skunk, coati, and badger (*Taxidea taxus*). As previously mentioned coyote and spotted skunk photos were almost exclusively recorded in desert scrub whereas hog-nosed skunk photos were associated with riparian forest. Coati, too, were exclusively associated with riparian forest (although this pattern may be more the result of sampling error than true habitat preference given that only four photographs of this species were recorded). Gray fox and striped skunk were habitat generalists, being photographed frequently in all habitat types.

Because remote cameras collect data on many species simultaneously, it may be possible to elucidate both positive and negative species associations. For example, we found a significant positive correlation between bobcat and coyote (correlation coefficient = 0.551, *p*=0.002). Although these correlations require experimentation to demonstrate causation, the camera data represent an important first step in elucidating these relationships. We also found a marginally significant correlation between puma photo rate and mule deer photo rate among cameras (correlation coefficient = -0.307, *p*=0.07). These data suggest avoidance of predation risk habitat by a prey species, or a landscape of fear effect (Laundre et al. 2010). Based on these camera data, we are now more closely examining puma and mule deer habitat segregation using pellet counts for mule deer and GPS collar data for puma.

Predation events are by their nature, difficult to observe. Remote camera arrays may record relatively rare events such as mammalian carnivore predation because they can operate continuously and for long time periods. This sort of monitoring could be of
particular use to managers dealing with nesting birds in areas where mesocarnivores are a management concern. Our remote camera data contains a surprising number of predation event data, and strongly suggests the efficacy of this tool for predation monitoring. The majority of our predation event data is for gray fox and appears to be the result of cameras placed near fox dens, as the photos tend to be concentrated at certain camera sites over short periods of time. In every case the fox is carrying a prey item rather than consuming it. We have documented fox carrying a wide variety of prey items, dominated by desert cottontails, followed closely by jackrabbits. Other prey items include packrats (*Neotoma spp*), quail, and doves. We also have one unusual photo of a gray fox with a large western diamondback rattlesnake (*Crotalus atrox*) in its mouth. Other predation event photos include coyote with desert cottontails, jackrabbits, and quail. Finally, we have two photos of a great horned owl capturing a gopher (*Geomvidae*).

In conclusion, we have demonstrated that remote camera arrays can be used as a cost-effective and critically needed management tool for detecting puma presence with quantifiable certainty as well as estimating unmarked puma populations comparable to mark-resight population estimates. The application of remote camera arrays for work with puma populations has tremendous financial and logistic benefits beyond puma management itself, as demonstrated by the wealth of information produced by the 18,000 + photo archive produced by our study. A wide variety of management and monitoring questions may be simultaneously addressed with remote cameras if proper planning and foresight is exercised. Furthermore, it has been shown that remote camera arrays may provide a cheaper tool for population estimates of other species (i.e. desert bighorn
sheep). Given the promise of our technique for providing critical information on puma populations as well as the myriad uses and benefits of remote camera arrays in wildlife management, we strongly encourage puma researchers with marked puma, or confident population estimates, to replicate our camera array design in order that the puma management and conservation community may confidently assess the potential for widespread application of this technique for improved and more responsible puma stewardship.
### Table 3.1. Results from and comparison of mark-resight and rate of encounter population density estimates. ²

<table>
<thead>
<tr>
<th>Population estimator</th>
<th>Population estimate</th>
<th>Effective area estimator</th>
<th>Effective area (km²)</th>
<th>Density estimate (#pumas/100 km²)</th>
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</thead>
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<tr>
<td><strong>Mark-resight</strong></td>
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<tr>
<td>daily</td>
<td>3.9 (3.2-5.9)</td>
<td>Camera MMDM</td>
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<td>2.1 (1.7-4.4)</td>
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<td>GPS MMDM</td>
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<td>0.36 (0.29-0.54)</td>
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<tr>
<td>grand</td>
<td>8 (7.1-12.4)</td>
<td>Camera MMDM</td>
<td>188</td>
<td>4.2 (3.8-6.6)</td>
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<tr>
<td></td>
<td></td>
<td>GPS MMDM</td>
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<td>0.74 (0.65-1.1)</td>
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<td><strong>Rate of encounter</strong></td>
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<tr>
<td>daily</td>
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<td>study area</td>
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<td>GPS MMDM</td>
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<td>0.17 (0.13-0.20)</td>
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</tbody>
</table>
Appendix B

Figures

Figure 2.1: Map of study area and 25-camera array
Figure 2-2: Map of example LM3 daily activity period kernel density showing the 95% homerange contour within the 25-camera array
Figure 3.1: This graph depicts the relationship between mean number of camera nights required for 95% probability of detection and camera number for a male (LM3) and female (LF1) puma. The male puma requires dramatically more camera nights than the female at low camera density. However, the difference in camera effort required to reach 95% detection probability between the two study animals decreases markedly as the number of cameras increases. For both puma, the number of camera nights required to reach 95% detection probability decreases as a negative power function with the number of cameras used.
Figure 3-2: This graph depicts the relationship between mean number of camera nights required for 95% probability of detection and camera number for a male (LM3) puma. As the number of cameras increases the mean number of camera nights required for 95% probability of detection decreases as a power function: \( Y = 1393.9X^{-1.042} \), \( R^2 = 0.82 \), \( p < 0.01 \)
Figure 3-3: This graph depicts the relationship between mean number of camera nights required for 95% probability of detection and camera number for a female (LF1) puma. As the number of cameras increases the mean number of camera nights required for 95% probability of detection decreases as a power function: $Y=69.243X^{-0.05}$, $R^2=0.82168$, $p<0.01$
Figure 3-4: This graph shows the relationship between mean pair wise distances (1 grid cell unit = 2 km) between different camera combinations by number of camera and probability of puma detection for one camera night for each combination of 1-25 cameras (trends for sampled combinations with 9 to 17 numbers of cameras not shown because of the large amount of processing space those analysis took up). The probability of puma detection for all number of cameras 2 to 24 slightly increased as the density of cameras decreased (puma detection probability for combinations of cameras with 9 to 17 cameras followed similar slight positive trends).
Figure C-1: Summary graph displaying the number of photos captured per mammal species for photo data collected from camera array maintained for 21 months of continuous data collection from April 29, 2008 to January 29, 2010.
LITERATURE CITED


