Jaguar Survey and Monitoring Techniques and Methodologies: A Review

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Table of Contents

Executive Summary **1**

Background **2**

Survey Designs and Statistical Analyses Applied to Data Collected During Jaguar Surveys, Monitoring, and Research **5**

Abundance and Occurrence 6

Species Distribution Mapping: Modeling presence-only data 7

Logistic Regression: Modeling presence-absence data 10

Occupancy: Modeling detection-non-detection data 11

Kinds of Occupancy Models 14

Capture-Recapture Models for Density Estimation Using Replicated Count Data 17

Poisson Encounter Model 19

Binomial Encounter Model 20

Density Estimation Using DNA 23

Estimation of Density When Animals Are Not Individually Recognizable 24

A Bayesian Approach 24

Random Encounter Models 26

Estimation of Density and Trends Using Unreplicated Count Data 28

Relative Abundance Indices 30

Power Analysis Fundamentals 32

Field Techniques Applied to Surveying and Monitoring Jaguars **33**

Sign 33

Tracks 34

Kills 38

Scats 39

Interviews 42

Remote Cameras 45

Designing Surveys 48

Refining the Design 52

Setting Camera Traps 54

Using Data for Indices of Species Not Identifiable to Individual Level 55

Occupancy Surveys 58

Additional Details on Survey Design and Analyses 59

Density Estimation 60
Hair Collection 62
Utility, Considerations, and Limitations of Hair Snare Techniques for Jaguars 63
Fecal DNA and Scat Detection Dogs 64
Sampling with Dogs 65
DNA analyses 65
Utility, considerations, and limitations of detection dogs 66
Telemetry 67
Ecological Monitoring 67
Population Monitoring 68
Population Genetics 70
Recommendations for Surveying in the Northwestern Recovery Unit 72
Summary and Closing Remarks 73
Literature Cited 74
Appendix 1: Jaguar Capturing and Handling 111
Background 111
Capture Methods 111
Hounds 112
Snares 113
Box Traps 114
Immobilization and Handling 114
Literature Cited 116
Appendix 2: Ecological Factors in Human-Jaguar Conflicts and Coexistence 121
Foundations 121
Prey Selection 121
Learned behaviors 122
Habitat selection 123
Foraging theory and management recommendations 124
Conservation Concepts 125
Interventions to reduce the impact of jaguar attacks on livestock 127
Interventions to reduce jaguar predation on livestock 127
Literature Cited 129
Appendix 3: Glossary 132
Literature Cited 135

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Executive Summary

Jaguars (*Panthera onca* L.) have lived in the America's for more than 2 million years, but thousands of years of range expansion were reversed in the last few hundred years, particularly on the northern margin of their range. In the United States, twentieth century records with photographic evidence, skins, and skulls are available from New Mexico, Arizona, and Texas, while twenty-first century observations are limited to southern Arizona and extreme southwestern New Mexico. Throughout this period, western Mexico has remained a harbor for jaguar populations supplying individuals to the United States. The pattern of retracting jaguar range in the historic northern limits of the species' distribution has been mirrored in the southern limits, and range retraction yet underway in much of jaguar range. The species is listed as Near-Threatened on the IUCN Red List, in Appendix 1 of the Convention on Trade in Threatened and Endangered Species of Fauna and Flora (CITES). The jaguar is recognized as an endangered species in Mexico (SEMARNAT 2010), and is a national priority for conservation (Ramírez-Flores and Oropeza-Huerta 2007). The U.S. Fish and Wildlife Service (USFWS) has determined that the jaguar is an endangered species throughout its range, including in the United States, under the definitions of the Endangered Species Act.

The 226,826-km² Northwestern Jaguar Recovery Unit (NRU) straddles the United States-Mexico border with approximately 29,021 km² in the United States and 197,805 km² in Mexico (Figure 1; Sanderson and Fisher 2013). The USFWS contracted the Wildlife Conservation Society to: 1) conduct a literature review of jaguar survey and monitoring techniques and methodologies; and 2) draft a jaguar survey and monitoring protocol for application in the NRU, and with relevance for monitoring the species range wide. In this first half of the task, we present the basics of jaguar monitoring.

Our introduction starts with a review of survey design and statistical analyses which includes the following: distribution mapping; occupancy modeling of detection/non-detection data; capture-recapture models for density estimation based on replicated count data obtained from camera traps and genetic samples; estimation of density when animals are not individually recognizable; estimation of density and trends using unreplicated count data, including a discussion of relative abundance indices; and the fundamentals of power analysis. We follow with a review of field techniques, which includes: sign (tracks, kills, scats), interviews, the use of remote cameras, hair collection for genetic analyses, scat detection dogs, capture and handling, and telemetry data. This entire gradient of methods is relevant to the NRU.

Jaguar conservation success in the NRU will depend upon execution of a comprehensive approach that applies a bi-national metapopulation perspective. The area's wealth of wild rugged terrain, possibilities of improved wildlife management, and increased appreciation of jaguars, translate to enormous potentials for recovery. The monitoring challenges posed in the NRU echo those encountered in much of jaguar range, where issues of scale, poor access, difficult logistics, and gradients of jaguar and prey abundance require a mix of sampling intensities. The

combination of core areas and the connections between them provides an exciting opportunity to design effective large scale monitoring.

Background

The jaguar is a large wide-ranging felid, whose presence or absence provokes strong feelings and conservation concern throughout the Americas (Medellin et al. 2002). Jaguars are the largest felids extant in the New World, with adults typically with head and body length of 1-2 meters and body mass from 36 to 158 kg (Seymour 1989). They are robust and successful predators, able to hunt, kill, and consume over 85 different wildlife species (Seymour 1989), as well as domesticated animals like cows and sheep (e.g., Rosas-Rosas et al. 2010), competing successfully with pumas (*Puma concolor* L.), and less so with human beings for prey (Rosas-Rosas et al. 2008). Jaguars occupy a wide range of habitats, from deserts to tropical rain forests (Seymour 1989, Sanderson et al. 2002); they stalk mountains up to 2,000 m and prowl beaches (Troeng 2001). It is not well understood what limits their range beyond the need for cover, food, some warmth, and freedom from human persecution (Seymour 1989, Crawshaw and Quigley 1991, Hatten et al. 2005).

Jaguars have lived in the Americas for more than 2 million years (Antón and Turner 1997, Brown and López-González 2001). Jaguars evolved in Eurasia along with the ancestors among the other roaring cats of the *Panthera* genus and immigrated across the Berengia land bridge, expanding across North America and into South America. Remains of jaguars from the Pleistocene have been found in North America from Florida, Georgia, Tennessee, Nebraska, Washington, and Oregon (Kurten 1980, Antón and Turner 1997). Human cultures, following the ancestral cats from Asia 1.9 million years later, formed strong cultural and spiritual affinities with the jaguar, especially in Central and South America (Benson 1998), and also in North America (see review by Merriam 1919, see Pavlik 2003).

Thousands of years of range expansion have been reversed in the last few hundred years, particularly on the northern margin of the range. The details of that loss, however, are in debate, especially in areas that are now the United States and Mexico (Sanderson and Fisher 2011). Accounts of the range collapse are complicated by the paucity of records and the different standards for scientific observation over the last 200 years, leading to lively debates about how range maps should be constructed, what different range maps imply for conservation actions, and how those actions interact with the language of specific statutes like the Endangered Species Act (Sanderson et al. in prep).

In the United States, nineteenth century written accounts (without accompanying physical proof or photographic evidence) of large spotted cats, possibly jaguars, exist from Louisiana, Texas, Oklahoma, New Mexico, Arizona, California, and Colorado (e.g., Sage 1846, Audubon and Bachman 1854, Whipple et al. 1856, Nowak 1973; see also reviews by Merriam 1919, Strong 1926, Brown and López-González 2001). A much smaller number of difficult-to-interpret, but

intriguing, observations are found from the eighteenth century from points much farther east than what is now commonly considered jaguar range in the United States (e.g., Brickell 1737, Jefferson 1780-1782[1905]). Twentieth century records with photographic evidence, skins, and skulls are available from New Mexico, Arizona, and Texas, and generally indicate a diminishing range within the United States (e.g., Schufeldt 1929, Brown and López-González 2001). Twenty-first century observations within the United States are limited to southern Arizona and extreme southwestern New Mexico (McCain and Childs 2008, Lacey 2011) and continue rarely but regularly to the present day (Arizona Daily Star 2013). Throughout the last 100 years, Mexico has remained a harbor for jaguar populations at the northern end of the range, especially in wilder parts of Sonora (Burt 1938, Leopold 1959, Landis 1967, Carmony and Brown 1991, Brown and López-González 2001, Grigione et al. 2009). Compiling this information and assessing it in various ways is a small cottage industry in the Southwest; numerous summary reviews of the observational history of jaguars over time have been published (Seton 1929, Goldman 1932, Householder 1958, Lange 1960, Brown 1983, Rabinowitz 1999, Brown and López-González 2001, Schmitt and Hayes 2003, Grigione et al. 2007), including a recent attempt to comprehensively document all observations in a searchable, relational database (Sanderson and Fisher 2011, 2013).

The loss of jaguar range in the United States and northern Mexico territory mirrors losses of range at the southern end of the range and in other places where human land use has driven out jaguar prey. Jaguars currently occupy 61% of their former pre-1900 range (Sanderson et al. 2002, Zeller 2007), which was once continuous from the southern United States to central Argentina (Swank and Teer 1989). It is not clear what biogeographic or climatological factors limit jaguar range (Sanderson and Fisher 2011). We do know that jaguars can be extirpated from areas through hunting for the fur trade, persecution in response to livestock depredation, and habitat loss (Swank and Teer 1989; Sanderson et al. 2002; Yackulic et al. 2011*a*, *b*). Though the fur trade stopped in the 1970s, direct killing has remained a significant source of mortality and population declines occur, especially where poorly controlled ranching overlaps areas where jaguars live and they learn to take livestock. Often in these situations, both control and indiscriminant killing ensues.

As a result of historic changes in jaguar distribution, habitat, and prey base, they are a species of conservation concern, listed as Near-Threatened on the IUCN Red List (Caso et al. 2011) and under Appendix 1 of the Convention on Trade in Threatened and Endangered Species of Fauna and Flora (CITES). The USFWS determined the jaguar is an endangered species throughout its range, including the United States, under the definitions of the Endangered Species Act of 1973 (U.S. Fish and Wildlife Service 1997). The jaguar is recognized as an endangered species in Mexico (SEMARNAT 2010) and is a national priority species for conservation (Ramírez-Flores and Oropeza-Huerta 2007). Despite these listing decisions and the protections they afford, jaguar populations throughout their range, and in the NRU, remain at risk from illegal killing of jaguars, habitat destruction and modification, overhunting of jaguar prey, and anthropogenic activities

reducing connectivity, limitations in enforcing regulatory mechanisms across national boundaries, and climate change (U.S. Fish and Widlife Service 2012).

In 1999, a range-wide meeting of 35 jaguar researchers and conservation practitioners conducted a range workshop that established an eco-regional basis for range-wide conservation of jaguars (Sanderson et al. 2002). The participants defined Jaguar Conservation Units (JCUs) as either: 1) areas with a stable prey community, known or believed to contain a population of resident jaguars large enough (at least 50 breeding individuals) to be potentially self-sustaining over the next 100 years, or 2) areas containing fewer jaguars but with adequate habitat and a prey base, such that jaguar populations in the area could increase if threats were alleviated (Sanderson et al. 2002).

At that time no jaguar populations were known in the United States (just a small set of recent observations) and the nearest confirmed JCU was in Sonora State, Mexico, about 80 km south of the border. The Sonoran JCU is listed as one of two highest priority JCUs in Mexico, and the only JCU representing that biome (ecosystem), thus enhancing its global conservation status. It is connected to pockets of potential habitat north of the border by dry, desert conditions, steep, mountain ranges, and sections of highway and border fence constructed to deter illegal human immigration and terrorism threats entering into the United States. The physical characteristics and anthropogenic activity (e.g., urbanization, roads, land development) may negatively impact connectivity for wildlife (Atwood et al. 2011), including for jaguars (U.S. Fish and Widlife Service 2012) yet jaguars have been moving through from Mexico into the United States (McCain and Childs 2008).

In 2005, the Instituto de Ecología de la Universidad Nacional Autonomo de Mexico (UNAM), with support of the Comisión Nacional de Áreas Naturales Protegidas sponsored its first national symposium on jaguar conservation (Chávez and Ceballos 2006). The current status of the jaguar in Mexico was assessed, threats to jaguar existence were identified, and priority conservation actions at local, regional, and national scales determined. Further, the need to conduct a population viability analysis and habitat assessment for jaguars in Mexico at a national scale was recognized (Carrillo et al. 2007). Subsequent, annual national symposia were held to develop an action plan to determine conservation strategies for the jaguar in Mexico, select methodology used for the National Jaguar Census (Chávez and Ceballos 2006, Carrillo et al. 2007), and outline general conservation guidelines for the jaguar and its habitat (Ramírez-Flores and Oropeza-Huerta 2007). A National Jaguar Census (CENJAGUAR) was started in 2008 in Mexico. The goal of the census is to estimate the population status of jaguars and jaguar prey in priority conservation areas in Mexico (Chávez et al. 2007).

Additional research, inventory, and monitoring programs were implemented in various parts of the jaguar's range (Chávez et al. 2007, Medellin 2009, Zarza et al. 2010, Caso et al. 2011, U.S. Fish and Widlife Service 2012, Panthera 2013). Within the NRU, recent surveys include López-González et al. (2000), López-González (2001), Navarro-Serment et al. (2005), McCain and

Childs (2008), Rosas-Rosas et al. (2008), Núñez-Pérez (2011), Gutiérrez-González et al. (2012), and Rosas-Rosas and Bender (2012). Despite these recent efforts, jaguar presence, occupancy, abundance, density, population trends, and demographic parameters are not well known, particularly in the NRU (U.S. Fish and Widlife Service 2012).

A monitoring program for jaguars and other large cats may have a number of objectives, with the most obvious and important being changes in area (range/habitat) occupied, and changes in abundance (numbers). A complete list includes: tracking trends in population size (space and numbers) over time; reproduction; estimating vital rates; understanding diet selection; understanding movements, habitat selection, limiting factors; and competition with other predators, including people. In designing a monitoring program, decisions must be made about which methods will generate the most critical information with the least cost, yet with defendable rigor that withstands scrutiny from scientific peers and spirited challenges from a full array of special interest groups. Particular methods may be best suited to specific sub-units within jaguar range. A one-size prescription will not fit all, since the charge is to monitor areas where jaguars are secure, relatively abundant, and dispersing (potential sources), as well as the less abundantly inhabited areas into which they are dispersing. A package of suitable methods is required to fit that gradient and measure those trends along that gradient. This literature review and the subsequent monitoring protocol are parts of that package. We will deliver, first, a review of literature pertinent to surveys and monitoring in general, and to jaguars in particular, addressing the conceptual and statistical frameworks for the most commonly applied survey and monitoring designs used by biologists and statisticians (this document). Secondly, we will deliver a prescription for a package of complementary methods that can measure trends in a cost-effective way across the gradient of core and secondary areas in the NRU, as well as range-wide.

Survey Designs and Statistical Analyses Applied to Data Collected During Jaguar Surveys, Monitoring, and Research

In wildlife ecology, a survey is a study conducted to collect data often over a broad spatial scale and through some sampling scheme (Williams et al. 2002, Long and Zielinski 2008, Boitani et al. 2012). Surveys are intended to define distribution, abundance, and other population attributes of species and their habitats at one time and in one area. Long and Zielinski (2008:8) defined a survey as "the attempt to detect a species at one or more sites within the study area, where 'attempt' involves one or more field sampling occasions, through proper methods, procedures and sampling design." Monitoring is the repetition of the same survey at the same location at more than one time to make inferences about changes in population status.

Every hypothesis requires an experimental design appropriate to answering the question it poses, and an analytical framework for drawing inferences from the data collected at an adequate level of accuracy and precision. When developing an analysis for inference from surveys and data, we must formalize the relationship between the data collected (usually some form of counts and covariates to explain counts) and the variable of interest (e.g., abundance or occupancy: Royle et

al. 2008). In this first section we restrict our discussion to the analyses of data most often collected for conservation purposes: abundance, occupancy, and density. Below, we provide a review of analyses, including strengths and weaknesses, of data of increasing complexity, from presence-only data to spatially-explicit capture-recapture (SECR) data.

Abundance and Occurrence

In the past 40 years or so, biologists and statisticians have developed a wide array of methods for estimating population size, density, occupancy, and demographic parameters (Williams et al. 2002). Most of these methods rely on counts corrected for detection probability. A count, *C*, can be considered a random variable that varies each time a sample is collected. E(*C*) is the expected value or average value of the count over a very large number of replicated samples. *C* relates to the population size, *N*, by the average probability of detection, *p*:

$$\mathrm{E}(C) = Np \tag{1}$$

If *p* can be estimated, then the parameter of interest *N* can be estimated as

$$\hat{\mathrm{N}} = \frac{c}{\hat{\mathrm{p}}} \tag{2}$$

This is the most basic population estimator and is known as the canonical estimator (Williams et al. 2002). When $p = 1$, $N = c$ and we have a census where the count equals the population size. If $p < 1$ but constant, the count tracks *N* accurately and can serves as a relative abundance index of population size. When detection probability is unknown and variable, then $\hat{p}$ must be estimated to establish the relationship between the count and estimated population size $\hat{N}$. The abundance estimator extends to an estimate of density, $\hat{\mathrm{D}}$, by defining a sampling area α, and

$$\hat{\mathrm{D}} = \frac{c}{\alpha\hat{\mathrm{p}}} \tag{3}$$

We can also estimate the proportion of an area that is occupied by considering *N* to be a population of sampling units, and *c* as the number of sampling units that we count as occupied, then the expected value of occupancy, ψ, when $p < 1$ is

$$\hat{\psi} = \frac{c}{\mathrm{N}\hat{\mathrm{p}}} \tag{4}$$

Survey methods may include sign surveys, including footprints, scat, and hair; presence-only data; presence-absence data without replication; presence-absence data with replication; spatially and temporally replicated count data on identifiable or unidentifiable individuals; unreplicated count data on unidentifiable individuals; and encounter data.

Species Distribution Mapping: Modeling presence-only data

Many recent techniques in species distribution modeling (SDM) rely on presence-only data, including maximum entropy models (MaxEnt: Phillips et al. 2004, 2006), genetic algorithms of rule set prediction (GARP: Stockwell and Peters 1999), ecological niche factor analysis (Hirzel and LeLay 2008) and others. Presence-only data arise under certain kinds of data collection. Use of museum specimens to re-construct species distributions often rely on location data for specimens because no data are available for where the specimens were not found. Presence data also arises when researchers are not confident that an absence reflects "true" absence; they drop the absence data and model the presence data. We found one case where the authors conducted a proper occupancy analysis but modeled habitat preference using presence-only data (Mondal et al. 2012), ignoring a considerable amount of information regarding the species distribution. Finally, proponents recommend use of presence only models for situations in which survey data tend to be sparse or limited in coverage (Elith et al. 2011). Use of presence-only data has increased significantly over the past decade from 4 publications in 2006 outlining the methods to 107 publications in 2012 (Web of Science search, 6 Sept. 2013). MaxEnt is arguably the most superior and widely used of these methods (Elith et al. 2006).

One of the motivating reasons for using presence only modeling for species distribution is that it avoids the problem of unreliable absence records, meaning it avoids the issue of "absent" versus "present but not detected." In MaxEnt, a landscape L is defined as a geographic area of interest, and L_1 is a subset of that landscape where a species is present (Pr(y=1)). Assume that a group of environmental variables $z_1, z_2, ..., z_n$, denoted by a vector **z,** are known for all locations $f(\mathbf{z})$ within L. Define $f_1(\mathbf{z})$ to be the relative likelihood of environmental covariates across locations within L_1 where the species is present, and $f_0(\mathbf{z})$ the distribution of environmental covariates in areas where the species was not detected (Pr(y=0)). The goal is to estimate the probability that the species is present, conditioned on the set of environmental covariates: $\Pr(y=1|\mathbf{z})$. Under Bayes Theorem, we find:

$$\Pr(y = 1|\mathbf{z}) = \frac{f_1(\mathbf{z})\Pr(y=1)}{f(\mathbf{z})} \qquad (5)$$

Elith et al. (2011) argue that the combination of presence data and background data allow the modeling of $f_1(\mathbf{z})$ and $f_0(\mathbf{z})$ to approximate $\Pr(y=1|\mathbf{z})$ to within a constant value Pr(y=1), the probability of presence. They argue that Pr(y=1), proportion of sites occupied, is not identifiable but can be estimated using the relationship $f_1(\mathbf{z})/ f_0(\mathbf{z})$. This ratio is called MaxEnt's raw output and it provides information about what environmental covariates are important and estimates the relative suitability of a one location versus another. To estimate Pr(y=1), they treat the $\log(f_1(\mathbf{z})/ f_0(\mathbf{z}))$ as a logit score and calibrate the logistic regression $\eta(\mathbf{z}) = \log(f_1(\mathbf{z})/ f_0(\mathbf{z})$ such that the intercept represents the probability of presence at sites with "typical" environmental conditions for species and is the same as the average value of $\eta(\mathbf{z})$ for $f_1(\mathbf{z})$. This intercept parameter, τ, is used as an estimate of Pr(y=1). If an estimate of τ is not available, τ is set to 0.5, meaning all

locations have a 50% chance of being occupied. If information on the likelihood of presence given sampling effort is available, it may be substituted for τ. To quote Elith et al. (2011), "The jaguar has very low local abundance even in suitable areas within its range, so a very small value τ is appropriate for all but the most intensive sampling schemes."

The assumptions underlying MaxEnt include: 1) sampling is either random or representative throughout a landscape (presence-absence surveys are less sensitive to this assumption); and 2) detection probability is assumed to be constant across sites (shared with presence-absence surveys). If sample selection or detection probabilities vary with environmental covariates and this variation is not quantified and included in the analysis, then it is impossible to separate the influences of these probabilities from occurrence. Elith et al. (2011) conclusions emphasize the importance of providing appropriate background samples, of dealing with sample bias, and of tuning the model—through feature type selection and regularization settings—to suit the data and application. They also recommend that if presence-absence data are available, it is advisable to use a presence-absence modeling methods. Such methods are less susceptible to problems of sample selection bias, often the survey method will be known and can be used to appropriately define the response variable for modeling.

Royle et al. (2012) provide a critical assessment of MaxEnt modeling and Yackulic et al. (2013) reviewed the use of MaxEnt in the literature. They stress that the random sampling assumption is critical when modeling presence-only data and that most applications of MaxEnt fail to consider the assumptions underlying the models. They show, using Bayes formula, that the probability of occurrence, Pr(y=1), is identifiable using maximum likelihood methods under the assumptions of random sampling and constant probability of detection. This undercuts one of the fundamental reasons for using applications like MaxEnt. They illustrate, using Breeding Bird Survey data and simulations, that MaxEnt suitability index is not proportional to the probability of occurrence and that MaxEnt produces biased distribution maps, underestimating the probability of occurrence in the center of the range and overestimating the probability of occurrence at the edges. The bias results from the MaxEnt model automatically setting τ to 0.5. Although Elith et al. (2011) point out that other values of τ may be more appropriate, there is no objective way to set the value of τ and no way to estimate τ from the data. Finally, Royle et al. (2012) provide a program, MaxLike, that gives a maximum likelihood solution for SDM using presence-only data.

Yackulic et al. (2013) evaluated 108 publications using MaxEnt modeling in terms of how well the studies described the modeling process and how well they met the assumptions necessary to derive reliable inferences from presence-only data. They found that 87% of the studies likely suffered from sample selection bias but did not attempt to control for this bias. They found that 37% of the studies discarded absence data although it has been argued that absence data should be used whenever it is available because discarding them results in a loss of information (Brotons et al. 2004, Ward et al. 2009, Elith et al. 2011). Most of the studies did not present information on the modeled relationships or model complexity but presented the model results as maps only. None of the studies reported estimates of τ, and all relied on the assumption that the

average probability of occurrence was 0.5. Most papers gave no a priori justification for how the covariates were chosen, or how the covariates were expected to be related to a species distribution. Incomplete reporting of methods and results makes it impossible to evaluate the results of these studies. Yackulic et al. (2013) conclude "All maps are partial truths, and when confronted with maps built from data that were obtained without any sort of sampling design and using complicated functional relationships, it is almost impossible to judge how well the map approximates reality."

MaxEnt modeling of large cat distributions is increasing in popularity. We found 6 publications using MaxEnt to model jaguar distributions (Torres et al. 2008, Rodríguez-Soto et al. 2011, Cuervo-Robayo and Monroy-Vilchis 2012, Ferraz et al. 2012, Tôrres et al. 2012, Jorge et al. 2013), as well as leopard (*Panthera pardus*; Mondal et al. 2013) and puma (Hernandez-Santin et al. 2012). Tôrres et al. (2012) argue that suitability values generated by SDMs are good indicators of habitat suitability, and should correspond to frequently occupied habitats (Thuiller et al. 2010). They test the hypothesis that suitability values are surrogates for density of a species across a large landscape. They model the potential distribution of jaguars throughout its range using 1,409 location points and compare the suitability scores to population density estimates at 37 locations. Their environmental covariate dataset included 10 climatic variables, elevation, and slope. They evaluated 11 SDM models, including MaxEnt. They document a wide range of model-dependent results, but generally a poor relationship between SDM suitability values and density. They postulate that the SDM-density relationship works well for high-density populations in high suitability areas, but low density can also arise in high suitability areas for reasons that are not modeled, such as disturbance and hunting. Practitioners of SDM recognize that model performance varies by species, that a number of models should be tried, and that the "best" model should be used. Best model criteria vary widely, but accuracy and precision appear not to be among the criteria.

Jorge et al. (2013) compiled presence records for jaguars (and three other species) in the Brazilian Atlantic forest biome between 2000 and 2012. They recorded patch location, species location, and patch size for 21 jaguar locations, as well as 11 environmental covariates, representing altitude, bioclimatic data, and landscape features. They created the model using (apparently) 13 points and 13 covariates, and tested the model using the remaining 7 points. They treated the logistic output as the probability of presence of suitable environmental conditions for the species, but they report the output as the probability of occurrence, assuming that $\tau = 0.5$. They incorrectly report in the results that all jaguars occurred in patches greater than 10,000 ha: at least 10 of 21 records occur in patches less than 10,000 ha (Figure 1 in Jorge et al. 2013). They found that 4 variables dominated the analysis, explaining 86% percent of variation in the model, but do not explain how the remaining covariates affected the model. This is an example of an over-specified model where the number of covariates approaches the sample size. An over-specified model tends to describe random error or noise instead of underlying relationships, and will generally have poor predictive power.

Logistic Regression: Modeling presence-absence data

Logistic regression (also known as binomial generalized linear model) is one of the most common statistical methods used in ecology (Royle and Dorazio 2008, Zuur et al. 2009). Logistic regression is used to predict the outcome of a categorical dependent variable, such as presence-absence data. The use of binary outcome data is appealing because it is simple to understand and efficient to collect across a large number of taxa and under a range of field conditions. Logistic regressions are useful because they can include covariates that help to explain sources of variation in the outcome. Consider a sample, c_i, on i = 1 to m sampling units. c_i = 0 if jaguars are not detected and 1 if jaguars are detected (present but not detected is not an outcome). Furthermore, consider that the ability to detect a jaguar is a function of rainfall (r), which might be reasonable if we are conducting sign surveys for jaguars in rainforests. c_i is distributed as a binomial variable with a probability p_i that $c_i = 1$ ($c_i \sim \text{Bin}(m, p_i)$). The mean value of c_i over m trials is mp_i with variance mp_i (1 - p_i). We also have some relationship to rainfall defined as $f(r_i) = \alpha + \beta r_i + \varepsilon$. If we define p_i to be a function of $f(r_i)$ then we have a linear regression $p_i = \alpha + \beta r_i + \varepsilon$. But the distribution of p_i is bounded by 0 and 1, and in linear regression, there are possible expected outcomes that include $p_i > 1$ and $p_i < 1$, so simple probabilities, bounded by 0 and 1, appear to be poorly modeled using linear regression.

In a logistic regression, we can convert the probability of detection p_i to the odds (O_i) of detection, which is the ratio of the probability of being detected to the probability of not being detected

$$O_i = \frac{p_i}{1-p_i} \tag{6}$$

The odds of detection have the advantage of not being bounded by 1, though it is still bounded by 0 on the lower end. If we then take the natural logarithm of the odds ratio, also called the log odds, it is no longer bounded by a lower or upper limit ($-\infty < \log(O_i) < \infty$). Log($O_i$) is also referred to as the logit link or logit (p_i):

$$\text{logit}(p_i) = \log\left(\frac{p_i}{1-p_i}\right) \tag{7}$$

In a logistic regression, we model the log odds as a linear function of the explanatory variable (rainfall) as $\text{Log}(O_i) = f(r_i)$ or logit (p_i) = $f(r_i)$. The entire logistic regression is given by:

$$c_i|\text{m}, p_i \sim \text{Bin}(\text{m}, p_i)$$

$$\text{logit}\ (p_i) = \alpha + \beta r_i$$

and

$$p_i = \frac{e^{\alpha+\beta r_i}}{1+ e^{\alpha+\beta r_i}} \quad (8)$$

Whatever the values of α, β, and rainfall, p_i lies between 0 and 1. This formulation has been very useful in ecology, and forms the basis for many habitat suitability studies and species distribution models. However, it does assume that detection is perfect (c_i = (0,1) with probability 1). When detection is imperfect, however, an observed zero becomes ambiguous, because it may arise from true absence (known as a structural or true zero) or from non-detection (known as a sampling or false zero). Logistic regressions usually work best when detection probability is high. We should consider, however, whether the assumption of perfect detectability in logistic regressions (and other applications) creates a problem. What is the impact of assuming perfect sampling coverage is complete (100% coverage)? Furthermore, when covariates are used in the modeling process, the effects of covariates are also underestimated, and the overall interpretation of results are uncertain.

There are not many examples of use of logistic regression in large cat research, despite its popularity as a tool for habitat suitability modeling. Hopcraft et al. (2005) used logistic regression to characterize lion kill sites in comparison to sites where lions scavenge carcasses. Ngoprasert et al. (2012) used logistic regression to examine distribution patterns of three large felids in Thailand. Other habitat evaluation studies include tigers (*Panthera tigris*; Imam et al. 2009), snow leopard (*Panthera uncia*; Wolf and Ale 2009), and leopards (Gavashelishvili and Lukarevskiy 2008). Logistic regression has also been used to characterize livestock depredation (Kolowski and Holekamp 2006, Suryawanshi et al. 2013) and attitudes toward predators (Holmern et al. 2007, Suryawanshi et al. 2013).

Occupancy: Modeling detection-non-detection data

When complete sampling coverage is not feasible, sampling programs face two sources of variation: space—often the area of interest is too large to be sampled completely so appropriate design principles must be used to select representative samples for proper inference; and detectability—few species are so conspicuous that individuals can be completely counted.

The logical extension of the binomial logistic regression is to consider three states, present and detected, present but not detected, and absent (MacKenzie et al. 2002, 2006). Assume that we sample a number of sites, *s*, from a study area composed of S possible sites, and all sites have the same probability of being occupied, ψ. The number of sites occupied (x) will follow a binomial distribution, as in the case of logistic regression with mean of sψ and variance sψ(1 - ψ). When detection is perfect (x_i = (0,1) with probability 1) we observe the true state of occupancy,

$$\hat{\psi} = \frac{\sum x_i}{s} \quad (9)$$

and

$$\mathrm{Var}(\hat{\psi}) = \frac{\psi(1-\psi)}{s} \tag{10}$$

Next, we assume the target species is detected imperfectly and the probability of detection is equal to *p* and known exactly. We now have three possible states, present and detected, present but not detected, and absent. The probability of being detected at least once on K replicated surveys will be $p^* = 1 - (1 - p)^K$. Because of incomplete but constant detection, we now have s_D sites where a species was detected out of *s* sites surveyed and

$$\hat{\psi} = \frac{s_D}{sp*} \tag{11}$$

and variance

$$\mathrm{Var}(\hat{\psi}) = \frac{\psi(1-\psi)}{s} + \frac{\psi(1-p^*)}{sp^*} \tag{12}$$

The variance now has two parts, reflecting the binomial variation associated with the true value of ψ, and the uncertainty in having to estimate the number of sites that were occupied in the sample. Similarly, when detection is imperfect and unknown, we must estimate ψ and *p* simultaneously using a maximum likelihood or Bayesian framework (MacKenzie et al. 2006, Royle and Dorazio 2008, Dorazio and Rodríguez 2012). In this case, ψ is estimated as above, and *p* is estimated as well. The variance of ψ then has a third component in addition to above that incorporates the uncertainty in ψ due to estimating p

$$\hat{\psi} = \frac{s_D}{sp^*} \tag{13}$$

$$\mathrm{Var}(\hat{\psi}) = \frac{\psi(1-\psi)}{s} + \frac{\psi(1-p^*)}{sp^*} + \frac{\psi(1-p^*)Kp(1-p^*)}{sp^*[p^*(1-p)-Kp(1-p^*)]} \tag{14}$$

Occupancy analysis has several attractive features. First, it provides unbiased estimates of ψ and *p* when modeling assumptions are met. *p* can be calculated when *p* is constant for the entire survey or can be calculated separately for each replicate of a survey. Constant detection might make sense when replicate surveys are conducted in a relatively short period of time during which environmental conditions remain fairly constant. Site-specific detection probabilities make sense when a given replicate is conducted at all sites within a very short time period, but there might be environmental changes between replicate surveys. The method is robust to missing values (survey sites are not surveyed on every occasion) that might arise either from logistical constraints or random events. If a site is not surveyed on a given replicate, then $p_{ij} = 0$ and the survey occasion is ignored for this site. Accommodation of missing observations means that equal sampling effort is not required across all sites. This allows for flexibility in sampling designs such as surveying at two levels of replication and removal designs where a maximum of K surveys are planned but sampling at a site stops when the species is detected and the remaining replications are treated as missing values (MacKenzie et al. 2002).

Occupancy analysis assumes that all sources of heterogeneity are accounted for in the modeling process. In many situations occupancy and detection are affected by environmental or anthropogenic factors that result in heterogeneity across the sampling units or within a sampling unit across replications. By using the logit link function, we can model occupancy as a generalized logistic regression with uncertainty whether the absence data represent absence or non-detection. The uncertainty is estimated by *p*. The probability that a site i is occupied can be modeled as

$$\text{logit}(\psi_i) = \alpha + \beta_1 x_{i1} + \beta_2 x_{i2} + \ldots + \beta_z x_{iz} \qquad (15)$$

which is a function of z covariates associated with *x* sites, an intercept α, and regression coefficients for each covariate. Covariates characterize a site and stay constant for the entire survey (site covariates). This satisfies the assumption that the occupancy condition of a site does not change during the season.

Detection probability *p* may be modeled in a similar way. We can consider two kinds of covariates. Site detection covariates remain constant over the season and may be the same or different than for occupancy covariates. Sampling covariates may change at a site over the sampling period due to changes that occur during the survey (weather, changes in observers, etc.). The probability of detecting a species at site i during survey j would be modeled as

$$\text{logit}(p_{ij}) = \alpha + \beta_1 x_{i1} + \ldots + \beta_z x_{iz} + \beta_{z+1} y_{ij1} + \ldots + \beta_{z+v} y_{ijv} \qquad (16)$$

where x's represent season-constant site covariates and the y's represent sample-specific covariates.

We advocate the balanced use of covariates to model heterogeneity in detection probability and occupancy, and to test hypotheses of interest to monitoring. Covariates may be measured in the field during sampling or may be assigned using global knowledge of the landscape (e.g., GIS information). If covariates are measured in the field, then the inferences using those covariates are strictly valid only for the area sampled because we cannot use the covariates to make predictions about areas not visited. If covariates based on some global knowledge (GIS, land-use, habitat, climate, deforestation) are known to be reliable for the site and are at an appropriate scale, then we can make predictions about expected occupancy of locations within the surveyed area that were not sampled. This approach is especially useful for species distribution and habitat selection modeling. It is important to include covariates that might affect detection probability because the models assume that all heterogeneity in detection is modeled and violation of this assumption can lead to biased inferences. Note that a modeling approach that involves finite mixture models provides an alternative for dealing with potential heterogeneity from an unknown source, i.e., when we do not have the appropriate covariate information. Ignoring covariates that might affect occupancy (e.g., habitat types) will reduce the precision of the estimates but should not induce bias. When evaluating management interventions or conservation effectiveness, we can stratify the landscape into treatments and calculate occupancy

separately for each treatment, then compare results. A more efficient alternative, however, is to treat the interventions as covariates within a single analysis. The nature of the objectives and the data may lend itself to one strategy over the other (see Kinnaird and O'Brien (2012) for examples of both strategies). For example, if law enforcement is one of our interventions, then we could stratify by law enforcement effort, e.g., none, low, medium, high, or alternatively assign a continuous variable value to each of the sampling units.

Occupancy modeling, as in any modeling exercise, requires that certain assumptions about the data and data collection are met (MacKenzie et al. 2006). These include: 1) occupancy status at each site does not change over the season of the survey (population closure); 2) probability of occupancy is constant across sites or changes in occupancy across sites is modeled with covariates; 3) probability of detection is constant across sites and surveys or differences are modeled with covariates; 4) detection of species and detection histories at each site are independent of other sites (no temporal or spatial autocorrelation); and 5) species are correctly identified (no false positives). If these assumptions are not met, then the estimates of occupancy and detection may be biased and inferences derived from these models may be incorrect. MacKenzie et al. (2006) and Royle et al. (2008) discuss the consequences of violations of assumptions, but the choice of model options available in occupancy modeling addresses many of the possible assumption violations.

Occupancy can be modeled in a multi-season framework, using the robust sampling design of Pollock (1982). This is very useful for studying the dynamics of occurrence over time and can be incorporated into monitoring programs (e.g., Karanth et al. 2006; Karanth et al. 2011). Under a multi-season model we would estimate occupancy in the first season, under the assumptions of a single season model. Between seasons, changes in occupancy and detection might occur. Occupied sites may become unoccupied (local extinction or ε) and unoccupied sites may become occupied (local colonization or γ). Colonization and extinction are the dynamic parameters (also called vital rates) for the state variable occupancy. The change in occupancy between time 0 and time 1 can be described by the relative effect of γ and ε on ψ_0: $\psi_1 = \psi_0(1 - \varepsilon) + \gamma(1 - \psi_0)$. Conservation interventions may affect occupancy over time through their effects on local colonization and extinction.

The strength of occupancy as a monitoring metric is its flexibility. We can model occupancy, point abundance, relative abundance, species richness, colonization, extinction, and detection as functions of covariates. Models incorporating different covariates may represent competing hypotheses about factors believed to affect occupancy, colonization, and extinction. Over time, multi-year models can be used to evaluate the effectiveness of conservation interventions.

Kinds of Occupancy Models

Single Season models—this is the basic occupancy model described above, which allows for simultaneous estimates of the proportion of the study area occupied and the detection probability

(MacKenzie et al. 2002). Occupancy and detection parameters may be constant across the sampling area or be estimated as a function of site and survey-specific covariates. Single season models based on mixture models (to deal with unobservable heterogeneity) can also be used. Substitution of species from a regional species list for sample units permits estimation of relative species richness in a study area and exploration of the covariates that affect species richness (MacKenzie et al. 2006). When covariates are used to estimate occupancy, predictive maps can be developed to include occupancy estimates for sites in which no detections were made and for sites that were not sampled (but fall within the study area and have covariate data) can be generated. Single season models can also be used for meta-population modeling.

Multi-season models—are an extension of single season models and can be used for inferences about occupancy over time and meta-population dynamics (MacKenzie et al. 2003). Sites can change between being occupied and unoccupied over time, allowing for estimates of rates of local extinction and local colonization. Single and multi-season models are ideal for large scale surveys of single species, single populations, meta-populations and communities when the sample units can be considered to contain discrete sub-populations.

Single season with false positive detections model—are useful when there is a good chance that sign, aural cues, or visual identifications are incorrect, violating assumption 5 (Royle and Link 2006, Miller et al. 2011). False positives are especially common in species richness surveys, sign surveys, and surveys that rely on aural identification. False positives also arise in camera trap surveys as a result of blurry photographs.

Multi-season with false positive detections model—are the extension of single season with false positive detection models.

Single season multi-method models—allow estimation of occupancy when more than one method for detection is employed across sites, providing detection probabilities for each method used (Nichols et al. 2008). This is useful for hybrid surveys or surveys using multiple cues such as species richness estimation for bird communities using visual and aural cues, or surveys for jaguars using multiple sign (footprints and scat).

Single season multi-state models—are used when we are interested in not only whether a site is occupied, but whether there are different states that the occupied site might attain (Nichols et al. 2007, Mackenzie et al. 2009). For example, we might want to evaluate the distribution of adult male, adult female, and non-breeding juvenile jaguars or evaluate the distribution of jaguars at different levels of abundance (habitat suitability analysis).

Multi-season multi-state models—extend multi-state models to multiple seasons (Mackenzie et al. 2009, MacKenzie et al. 2011). For example, occupancy models can be used to estimate if a species is *absent*, *rare*, or *abundant* (i.e., 3 population states) or, alternatively, if different life history stages are present, such as: *absent*, *juvenile*, *adults*. When used in multi-season models,

we can estimate meta-demographic rates such as colonization, extinction, reproduction, and recruitment.

Multi-season integrated habitat occupancy—can be used to examine how habitat suitability and factors that affect habitat suitability can influence the distribution and relative abundance of organisms over time (Mackenzie et al. 2009). This model has been used evaluate occupancy and relative abundance of elephants at water holes in Zimbabwe (Martin et al. 2010) and would be a good candidate for comparing track or dung surveys over time.

Single season 2 species co-occurrence models—are used when the goal is to determine if 2 species occupy a site, whether occupancy is affected by co-occurrence, and to assess whether they affect each other's detection probabilities (MacKenzie et al. 2004). We can also test if the detection probability of one species changes in the presence of the other. This model would be useful to compare co-occurrence between jaguars and other predators or prey.

Multi-season 2 species co-occurrence models—are the extension of single season 2 species co-occurrence models.

Repeated count models—are occupancy based abundance estimation procedures used to estimate the number of individuals at a point when individuals cannot be identified or marked (Royle 2004). Rather than using species presence-absence (detection-non-detection) data, these models are based on counts of individuals obtained at replicate visits. These can be very useful when the sample sites are discrete (e.g., ponds or woodlots) and where the area of sampling can be defined (e.g., fixed distance point count).

Single season abundance-induced heterogeneity models—are similar to above but based on the idea that heterogeneity in abundance generates heterogeneity in detection probability (Royle and Nichols 2003). These use presence-absence data to estimate point abundance, and occupancy as a function of point abundance.

Single season staggered entry models—are used when we cannot assume that the population is closed within a season, violating assumption 1 (Kendall et al. 2013). Instead, individuals of the species are assumed to arrive and depart from the study area. We estimate P(arrival), P(departure), and P(detection) to develop occupancy estimates.

Single season spatial/temporal autocorrelation models—are used when we have correlated observations, either spatially or temporally, violating assumption 4 (Hines et al. 2010, Bled et al. 2011). When conducting sign surveys along trails or when using camera traps, we may encounter situations where observations are correlated in space or time. These models incorporate autocorrelation in detections to produce unbiased occupancy and detection estimates.

Multi-seasonal with spatial dependence models—extend the spatial/temporal autocorrelation model to multi-season sampling with spatial or temporal correlation within seasons.

Multi-season heterogeneous detection—multiple season "mixture" model, which assumes sites belong to one of two unidentifiable groups (with different detection probabilities).

Capture-Recapture Models for Density Estimation Using Replicated Count Data

When individuals of a species can be recognized, either through natural or applied marks, then these individuals can be "captured" (identified) and then "recaptured" (subsequently re-identified during sampling) over a series of sampling occasions. In this manner, we can develop capture histories that characterize the individual's occurrence in sampling over time (and space) that can be used to estimate abundance. Abundance estimation using individually recognizable animals has a long history dating back to Peterson's (1896) original formulation of the concept and Lincoln's (1930) application to waterfowl. Today we have a large number of closed and open capture-recapture models and software packages for implementation in a maximum likelihood (CAPTURE: Otis (1978); MARK: Cooch and White (2006)) and Bayesian framework (Royle and Dorazio 2008). There have been many reviews of capture-recapture abundance modeling, both general (Seber 1982, Skalski and Robson 1992, Williams et al. 2002, O'Brien 2011) and for species-specific monitoring (tigers: Karanth and Nichols (2002); leopards: Henschel and Ray (2003); jaguars: Noss et al. (2013); elephants: Hedges et al. (2013)). In this section, we focus on the issue of density estimation using capture-recapture data from trapping arrays.

A persistent problem with abundance modeling using capture-recapture data was the issue of converting abundance to density, a conversion that is necessary for comparing estimates between sites. Although population closure in time has been well recognized as a necessary assumption for abundance estimation, the lack of a geographic barrier (closure) around a study area means that animals can easily move on and off the area of interest (White et al. 1982). This phenomena is known as temporary emigration (Kendall and Nichols 1995, Kendall et al. 1997) and leads to underestimation of detection probability and over-estimation of abundance. Trapping arrays with ill-defined spatial borders affect the individual heterogeneity in detection because animals on the edge of the trapping array have a lower exposure to traps than animals in the center of the trapping array. Temporary emigration highlights the problem of delineating the effective sampling area from which animals are exposed to trapping (Royle and Young 2008).

Otis (1978), following on Dice's (1938) idea, recommended adding a strip of width W to the convex polygon defining the outer limits of a trapping grid to reflect the area from which animals are sampled, in order to convert an abundance estimate to a density estimate. Unfortunately, there was no standard method for estimating W, leading to a number of *ad hoc* methods (O'Brien 2011). Parmenter et al. (2003) evaluated several methods of estimating density from rodent capture-recapture sampling designs, including DISTANCE-based trapping web, 1/2 the mean maximum distance moved (1/2MMDM model: Wilson and Anderson (1985)), and full mean maximum distance moved (MMDM) model. They found that the trapping webs gave accurate but equivocal results and the full MMDM yielded accurate but imprecise density estimates. Soisalo and Cavalcanti (2006) compared jaguar density estimates based on radio telemetry,

1/2MMDM, and MMDM, and found that use of 1/2 MMDM models underestimated the diameter of a home range, leading to overestimates of density, but MMDM models approximated density based on the distribution of collared jaguars. However, all MMDM methods are constrained because the distribution of possible movement distances is constrained as a function of distances between traps. Applications of MMDM therefore may underestimate width of the *W* on a limited trap array, and hence overestimate density.

Recognizing the problems that arise from edge effects and the *ad hoc* estimation of *W* from trapping data, as well as the uncertainty and logistical difficulties associated with web-trapping designs, Efford (2004) proposed a combination of Monte Carlo simulation and inverse prediction methods (Pledger and Efford 1998) to estimate jointly the population density and two parameters of individual detection probability directly from capture-recapture data. The model assumes stationary home ranges that are of equal sizes with centers that are Poisson-distributed with density *D*. The probability that an animal is detected in a trap at distance *r* from its home range center is described by a 2-parameter spatial detection function *g(r)*, usually a half-normal distribution with parameters g_0 when $r = 0$ and σ is a scale measure of home range size. *D*, g_0 and σ define the detection process. Monte Carlo simulation is used to match the parameters to the statistics calculated from the capture-recapture study ($\hat{N}$, $\hat{p}$, $\bar{d}$). An inverted linear model is then used to predict the values of the parameters (D, g_0, σ) from the field data. In addition to the normal closed population assumptions, density estimation assumes that animals occupy stable home ranges and that capture does not affect the probability of recapture. The method is robust to choice of: 1) abundance estimator (including the number of individuals caught [M_{t+1}]: Efford et al. (2004, 2005)), 2) trapping configuration, and 3) number of traps, and produces unbiased estimates of density when the assumptions are met. Borchers and Efford (2008) developed a maximum likelihood solution for SECR models. A software program, DENSITY (Efford et al. 2004), implements both the model-based and maximum likelihood methods.

Following much work on a Bayesian approach to hierarchical capture-recapture models using the technique of data augmentation, Royle et al. (2007), Royle and Dorazio (2008), and Royle et al. (2009) presented a framework for a Bayesian approach to density estimation via a SECR framework. The derivation is similar to Borchers and Efford's (2008). Here we summarize the maximum likelihood and Bayesian modeling approaches, following Royle and Gardner's (2011) review.

Density estimation replaces the estimation of number of individuals exposed to trapping (*N*) with a hierarchical model that considers the distribution of individuals in space (activity centers or home range centers) and the imperfect observations of encounters of individuals with traps. The goal is to develop a model that describes the spatial organization of individuals in relation to how they are observed (Royle and Gardner 2011). First, assume that individuals are represented by fixed points in space s_i, $i = 1, 2, \ldots , N$, distributed over some area S, which can be much greater than the area of the trapping array. The point locations are fixed during sampling and are

described by a point process model, usually a Poisson, Binomial, or Uniform model. Borchers and Efford (2008) suggest a Poisson process model that is not conditional on *N*, whereas Royle and Young (2008) recommend a binomial point process model that is conditional on *N*. Individual activity centers are not observed and are considered latent (unobserved) variables in the model. Sampling is achieved using an array of *J* traps with locations x_j, $_j$ = 1, 2, ..., *J*. The probability that an individual is captured in some trap is a function of the distance between its activity center and the trap, and one or more parameters to be estimated. Density estimation therefore reduces to estimating the number of activity centers in the area S.

Capture histories are generated as a 3-dimensional array. An observation y_{ijk} is generated when individual *i* is observed (1) or not observed (0) at trap *j* during trapping occasion *k*. Traps are capable of capturing more than one individual within a sampling occasion, and individuals may be captured more than one time at a trap and at multiple traps within a sampling occasion. Typically, multiple captures at a single trap within a sampling occasion are collapsed into a single detection. Three kinds of observation models are considered: 1) the Poisson model in which individuals can be caught multiple times in multiple traps; 2) the Binomial model in which an individual can be caught only once in a trap but can be caught in multiple traps; and 3) the Multinomial model in which an individual can be caught only once in a trap and only in one trap per sampling occasion. Models 1 and 2 are appropriate to passive sampling like camera trapping, whereas model 3 is appropriate to trapping studies involving live traps such that capture at a trap precludes visiting another trap during the sampling occasion. Model 3 will not be discussed further.

Poisson Encounter Model

For an observation y_{ijk}:

$$y_{ijk} \sim \text{Poisson}(\lambda_0, g_{ij})$$

where λ_0 is the baseline encounter intensity and g_{ij} is a decreasing function of distance between trap and activity center. For a trap located at an individual's activity center, λ_0 is the expected number of captures in that trap. Royle and Gardner (2011) only consider a half-normal distribution, but other distributions (e.g., hazard function) might be used. For the half-normal distribution:

$$g_{ij} = e^{\frac{-d_{ij}^2}{\sigma^2}} \tag{17}$$

where σ is a scale parameter for home range size and *d* is distance from trap location to activity center. As *d* increases, the probability of detection at the trap declines. This formulation can be expressed as a Poisson regression with d_{ij}:

$$\log(\mathrm{E}[\mathrm{y_{ijk}}]) = \log(\lambda_0) - \frac{1}{\sigma^2}(d_{ij}^2) \tag{18}$$

Binomial Encounter Model

The binomial encounter model reduces the number of encounters that might have been observed under the Poisson model to a simple binary (0,1) variable. This might be useful when an individual may be encountered multiple times, but the encounters cannot be unambiguously identified (hair samples, camera trap photos within a sampling occasion). In this case, for an observation y_{ijk}, the probability that y>0 (or equivalently Pr(y=1)) is:

$$\pi_{ijk} = Pr(y_{ijk} = 1) = 1 - e^{-\lambda_0 g_{ij}} \tag{19}$$

This model can be represented as a binomial generalized linear model with a linear effect of distance *d* on the detection probability π_{ijk}:

$$\log(-\log(1 - \pi_{\mathrm{ijk}}) = \log(\lambda_0) - \frac{1}{\sigma^2}(d_{ij}^2) \tag{20}$$

Borchers and Efford (2008) define density *D* intensity of a Poisson spatial point process for *s* unknown but fixed home range centers. The data comprise a set of *n* detection histories for the observed individuals. The probability of observing a particular capture history *i* depends on a vector of detection parameters and the unknown activity center of individual *i*. The unknown centers are integrated out of the likelihood using non-null detection histories (individual detected at least once) and the probability density of activity centers given that the animal was detected. The integration is carried out over the area of interest S. The density is then calculated as *n*/*a*, where *n* is the number of unique animals detected during the survey, and *a* is effective sampling area. Effective sampling area is defined as the size of an area in which the expected value of *n* is the same as the actual value of *n* for the survey when all animals within the area are detected and no animals outside the area are detected.

The Bayesian approach first assumes a uniform prior distribution for *s* activity centers over some region S (s_i ~ Uniform[S]) which is equivalent to describing the limits of integration above. Because *N* is unknown, the model requires that prior distributions for *N* (number of activity centers), λ_0 (expected number of detections at *d*=0), and σ (shape parameter for half-normal distribution) be specified. They assume a prior distribution for σ as Uniform(0,5) and λ_0 as gamma(0.1,0.1), both reflecting the absence of prior information about the parameters. To specify *N*, Royle et al. (2007) used the method of data augmentation. They recognize that *N* is unknown but greater than the observed *n* capture histories. They assume a discrete uniform prior distribution on the integers 0, 1, ... , *M* for some large value of *M*. Data augmentation considers the *n* observable detection histories, and then adds an arbitrarily large set of *M*-*n* "all zero" detection histories. This method creates a zero-inflated version of the model for a complete data set assuming that *N* is known.

The process of data augmentation therefore begins by considering a super-population of size *M*, in which some portion of the population has all-zero detection histories because they are exposed to trapping and not detected (structural or true zeros), or because they were not exposed to trapping (sampling or false zeros). A discrete uniform prior distribution for *N* also can be defined by N ~ Binomial(M, ψ), and assuming a uniform prior distribution for ψ ~ Uni(0,1). When ψ is removed from the binomial portion by integration, the remaining distribution is N ~ Du(0,M). The superpopulation can be described by a set of latent indicator variables $z_1, z_2, ..., z_M$ where z_i = 1 if the individual is a member of the population exposed to trapping, and $z_i = 0$ if the individual is not in the population exposed to trapping. We assume that z_i ~ Bernoulli(ψ). The model is specified in terms of the zero-inflated "known-N" model. For example, y_i ~Poisson(λ_0,g_{ij}) if z_i = 1, $y_i = 0$ if $z_i = 0$. The model is analyzed using Monte Carlo Markov Chain methods in WINBUGS. The output gives an estimate of ψ, the probability that M members of the superpopulation are part of the population exposed to trapping in area S (ψM = N[S]). Density is then the population size (N[S]) applied to the area of interest (S).

Software packages are available for both maximum likelihood and Bayesian calculation of density. Maximum likelihood solutions can be calculated in DENSITY5.0 (release December 2012) or SECR 2.6.1 in R (release June 2013). Bayesian solutions can be calculated in WINBUGS (Royle and Dorazio 2008) or in SPACECAP in R (Gopalaswamy et al. 2012*b*). Density 5.0 offers a broad range of model specifications, including specification of the distribution model and detection model, specification of g_0 and σ as a function of time, capture response, individual heterogeneity and trap response. DENSITY 5.0 also treats open and closed population models. The R package SECR 2.6.1 (release June 2013) includes most of the features of DENSITY 5.0, but also expanded options for detection, specification of Poisson distribution with covariates for home range centers, integration of telemetry with capture-recapture, and model averaging. The R package SPACECAP 1.0.6 (release June 2012) allows modeling of individual heterogeneity models with a covariate for habitat suitability for potential activity centers. Model specification includes trap response, and specification of encounter distribution (Bernoulli or Poisson). The detection function is assumed as a half-normal.

Applications of SECR for estimation of density of forest carnivores first appeared in the literature in 2009 (Royle et al. 2009*b*). Karanth, Nichols, Royle, and others have used Nagarahole tigers (India) as a test data set to develop a wide range of analytical techniques for abundance and occupancy estimation, including Bayesian estimators for abundance and density. Gerber et al. (2010) compared 1/2 and full MMDM estimates to SECR estimates using DENSITY for two endemic Madagascar carnivore species. They found (as have most others) that MMDM and SECR estimates were similar but that 1/2MMDM overestimated density. O'Brien and Kinnaird (2011) performed a similar comparison for four African carnivores using a standard trap array rather than a trap array specific to a single species. They found that full MMDM density estimates based on heterogeneity models (M_h and finite mixture models) compared well to one another, but that SECR models produced comparable or higher densities.

O'Brien and Kinnaird (2011) also showed that precision of the density estimates was lower than for the standardized trapping array compared to trapping arrays targeting tigers (Royle et al. 2009*b*), probably due to differences in estimating detection probabilities using a design to optimize detection among multiple species versus a design that maximizes detection of a single species.

Sollmann et al. (2011) were the first to apply data augmented Bayesian SECR models to jaguars, incorporating sex-specific parameters to account for differences in use of space by males and females. Recently, there have been a number of papers reviewing survey design and (to a lesser extent) analysis for capture-recapture studies of large cats, many focused on jaguar surveys (Maffei et al. 2011*a*, Foster and Harmsen 2012, Sollmann et al. 2012*a*, Noss and Maffei 2013, Tobler and Powell 2013). Maffei et al. (2011*a*) and Foster and Harmsen (2012) focus on similarities and differences between jaguar survey designs, potential for biased estimation, and do not discuss analytical techniques in detail except for density estimation using CAPTURE and MMDM methods. Both reviews recommend that survey areas be increased, a common theme of all the reviews.

In reviewing results of surveys in Mesoamerica, Maffei et al. (2011*a*) note the issues that variable design caused in being able to separate sampling noise from valid population differences, and provide recommendations which included greater standardization and increased sample area sizes. Noss et al. (2012) compared results obtained using CAPTURE, DENSITY, and SPACECAP. They noted: 1) the potential for biased overestimates when analyzing small sample areas using CAPTURE and *ad hoc* sample area estimates, 2) reduced density estimates with spatially-explicit models, and 3) the suggestion of convergence of results between all three models (CAPTURE, DENSITY, SPACECAP) when sample areas became really large, reducing previous sources of bias. Tobler et al. (2013) used a model similar to Sollmann et al. (2011) to estimate jaguar densities in optimal habitat in Peru. They point out that the tendency of researchers to use small sample grids in jaguar surveys (under 100 km^2) may lead to low precision and biased estimates of density, and that when large differences in ranging patterns occur, due to sex or age differences, then models should incorporate these differences.

Sollmann et al. (2012) used simulation studies to evaluate the effect of spatial distribution and size of trapping arrays on SECR parameter estimates. SECR models performed well as long as the extent of the trap array was similar to or larger than the extent of individual movements. SECR performed well across a range of spatial trap setups (trap density, array sizes) and movement patterns. They conclude that SECR models are more appropriate for the study of wide-ranging mammals and more flexible for designing studies that target multiple species. Tobler and Powell (2013) compared simulated density estimates for jaguars to assess how well MMDM density models compared to SECR models by assessing the bias due to sampling designs. They confirm that the best results for density estimation come from SECR and M_h with full MMDM models, and that the size of the trap array is important. They also found that using simulated values for σ, or borrowing information from several studies to estimate σ could correct

biases associated small size of trapping array, suggesting that proper estimation of the scale (home range) parameter σ is an important aspect of SECR density estimation. Finally, a recent camera trap manual (Noss et al. 2013) provides an excellent summary of many of the issues covered in the reviews and simulation studies, incorporating them into a comprehensive manual for designing, executing, and analyzing camera trap capture recapture studies.

Density Estimation Using DNA

Although we have focused on sampling issues related to camera trapping in this section, the methods are equally applicable to analysis of DNA identified from hair samples or recovered from scat obtained from area searches (Royle and Young 2008, Gardner et al. 2009, Efford 2011). DNA-based capture-recapture studies are broadly similar irrespective of the DNA medium sampled (hair, scat, feathers). Samples containing DNA are collected, often non-invasively, at several points in time, DNA is extracted and genotypes (individual identities) are typed. Lukacs and Burnham (2005) review many of the issues associated with identifying genotypes from field-collected DNA. Matching genotypes are considered as arising from the same individual and classed as recaptures and the analysis proceeds in a mark-recapture framework. Standard capture-recapture models have an assumption that individuals are always identified correctly, and that samples come from some sort of trap array. In data collection for genetic sampling, identification may be faulty due to lack of genetic information in the sample or genotyping error, and samples may result from trap arrays or from area searches.

DNA samples can be characterized by uncertainties associated with individual identifications, giving rise to false positives when a genetic sample is misidentified. Such uncertainties, when ignored, can lead to biased estimates of abundance and density (Lukacs 2005, Lukacs and Burnham 2005*a*, *b*). False positives increase the apparent number of individuals detected only once in a survey, causing p to be underestimated and the population estimate to be overestimated. Fortunately, model-based approaches to incorporating identification uncertainty into capture-recapture inference have solved the problem of genotyping error (Lukacs and Burnham 2005*a*, *b*).

Sampling designs for capture-recapture in trap arrays have already been discussed above. Royle and Young (2008) and Efford (2011) discuss density estimation when the samples are collected in the area of some polygon, all individuals detected within the polygon are marked, and replications involve repeated searches of the polygons. Searches along transects are considered a subclass of these models. For a trap array, detection probability is modeled as a decreasing function of the distance between the animal's home range center and the trap. For searches of a polygon, the probability of detection is a function of the overlap between the home range and the polygon (i.e., the probability that an animal is within the polygon). Assume that p_{sk} represents the probability of detecting a particular animal in polygon k on occasion s. Detection depends on the location, size, and shape of the animal's home range relative to the polygon, and on the efficiency of detection while the animal/DNA is within the polygon. We model the possible

locations of an individual in a home range with a circular bi-variate normal distribution $h(u)$ where $u = (x,y)$ and σ is the scale parameter. Efficiency of detection is controlled by the parameter p_∞, which is interpreted as the probability of detection when a home range is completely contained within a search polygon. The model development proceeds as for the points in a trap array, but the solution is applied over the area of each search polygon. Royle and Young (2008) used Bayesian methods and data augmentation to estimate flat-tailed horned lizard densities in a 9 ha polygon (single search area) and Efford (2011) used the same data for the Maximum likelihood example and showed that both gave similar results. Efford (2011) reported that methods work best when the search polygon approximates the home range size of the target species, and the number of replicated identifications exceeds 20. If the species leaves multiple cues (feces or hair samples) in a polygon, then it is not necessary to make replicate collections in a polygon.

Mondol et al. (2009) developed a rigorous set of captive, laboratory, and field protocols for identifying individual tigers through fecal DNA. Subsequently they compared genetic capture-recapture estimates to results from photographic capture-recapture estimates from the same site in dry forest in India. The close match of the estimates recommends genetic sampling as an additional tool for abundance in areas where densities are low and camera trapping may be impractical due to environmental constraints or logistical challenges (Mondol et al. 2009). Aided by a scat detecting dog in Belize, Wultsch et al. (2011) developed protocols for sample collection and storage in the warm and humid tropics, testing amplification success rates from four different locations in scats and comparing results from different storage techniques. The authors optimized a set of 14 highly variable microsatellite primers to estimate sex ratio, genetic structure, and variability of felid populations across multiple study sites on a country-wide scale. The felids were also sampled with remote camera traps to compare the results, the formal publication of which is still pending.

Estimation of Density When Animals Are Not Individually Recognizable

A Bayesian Approach

Although estimation of abundance and density is well understood when the species of interest is a population of individually recognizable animals, more often the species of interest has no distinguishing features (other than its DNA) to assist in identification. Chandler and Royle (2013) developed a spatial capture-recapture model without individual identity that estimates density from spatially-replicated point counts, making use of spatial correlation among counts. The model combines SECR and N-mixture models to address the problem of spatial closure and the inability to identify individuals simultaneously. The data required are spatially-indexed counts made on replicated sample occasions in an array of closely-spaced sample units such that the same individuals can be encountered at multiple locations. They utilize the spatial correlation in counts to provide information about the location of individual activity centers, which enables estimation of density and distance-related heterogeneity in detection. The model is applicable to

a wide range of samples of interest to jaguar biologists, including camera traps, hair snares, and track plates. It is also useful for closely spaced trapping arrays and when the camera traps collect a combination of recognizable and unrecognizable jaguar images.

The model closely resembles a Bayesian SECR model. First assume that activity centers are distributed over S, with s_i denoting the coordinates of the activity center (s_{i1}, s_{i2}) and distributed as uniform over S. Let z_{irt} be the encounter frequency of individual i in trap r during occasion t. Then the encounter model is similar to the Poisson encounter model:

$$E(z_{irt}) = \lambda_{ir} = \lambda_0 e^{\left(\frac{-d_{ir}^2}{2\sigma^2}\right)} \tag{21}$$

where λ_0 is the expected encounter rate at $d = 0$ and σ is the scale parameter related to home range. σ also relates to the degree of spatial correlation among counts because animals with large home ranges are more likely to be counted at multiple traps than animals with small home ranges. Because individuals cannot be observed directly, the encounter frequencies as considered latent variables from a Poisson distribution with mean λ_{ir}:

$$z_{irt} \sim \text{Poisson}(\lambda_{ir})$$

Normally the z_{irt} are the observed data, but when individuals cannot be recognized, the observed sample totals and trap-specific totals are summed over all unknown N individuals and n_{rt} is the number of individuals observed at trap r on occasion t. Furthermore:

$$n_{rt} \sim \text{Poisson}(\Lambda_r)$$

$$\Lambda_r = \lambda_0 \sum_i e^{\left(\frac{-d_{ir}^2}{2\sigma^2}\right)} \tag{22}$$

We can aggregate the replicated counts for trap r over t sampling occasions defining

$$n_r = \sum_t n_{rt} \tag{23}$$

$$n_r \sim \text{Poisson}(T\Lambda_r)$$

Because N is unknown, Chandler and Royle (2013) use data augmentation to specify N in terms of individual Bernoulli trials and assume $N \sim \text{DUniform}(0,M)$ for some large value of M, $N|M,\psi \sim \text{Binomial}(M,\psi)$ and $\psi \sim \text{Uniform}(0,1)$. Finally, they introduce a set of latent variables $w_i \sim \text{Bernoulli}(\psi)$, such that the model implies that if $z_{irt} > 0$, $w_i = 1$, and when $z_{irt}=0$, $w_i=0$.

Under this formulation the model is a zero-inflated version of the original model and

$$N = \sum_{i=1}^{M} w_i \tag{24}$$

and

$$D = \frac{N}{A(S)} \tag{25}$$

Where A(S) is the area of interest.

A simulation study demonstrated that the posterior mode is an accurate point estimator as long as the trap spacing is not too large relative to scale parameter σ of the detection function. Marking a subset of the population can improve precision, so this method should be useful for estimating density of jaguars when the trapping grid is small relative to range size and the data contain clear and unclear identifications. This is the first demonstration that spatial independence and individual recognition are not *required* to estimate population density. Spatial dependence induced by design can be informative about individual distribution and density. This analysis has been used for estimating the density of calling parula warblers (*Setophaga americana*) using replicated point counts, but has not been applied to large cats or their prey. Sollmann et al. (2013) comment that this model is sensitive to model assumptions and trap design; however, the same can be said for most (or all) of the spatial capture-recapture analyses.

Random Encounter Models

In principle, encounter rates can contain information about density (Hutchinson and Waser 2007, Chandler and Royle 2013, contrary to Sollmann et al. 2013). We know, for example, that detection probability increases as local abundance N_i increases ($p_i = 1 - [1 - r]^{Ni}$: Royle and Nichols (2003)). Several examples of abundance indices based on camera trap encounter rates and calibrated to independent estimates of density can be found in the literature (O'Brien et al. 2003, Rovero and Marshall 2009, Kinnaird and O'Brien 2012) that suggest a relationship does exist between encounter rates and abundance, though that relationship is elusive and may be unique to each situation. Jennelle et al. (2002) recommended a method to estimate density from encounter rates would be to model the underlying observation process. This approach is similar to the SECR modeling approaches already discussed in that the spatial distribution and observation process are modeled together. Here, we briefly consider circumstances in which we collect count data (encounters) with unidentifiable animals. Encounters may be in the form of track lines crossing a transect (Formoroz-Malyshev-Pereleshin model: Stephens et al. (2006)) or animals encountering a camera trap (Random Encounter Models: Rowcliffe et al. (2008)). Encounters are modeled as a random encounter point process using random gas models (Hutchinson and Waser 2007) to predict collision rates in an ideal gas contained in a vessel.

The classic two-dimensional random gas model assumes two species of molecules colliding whenever circular zones of contact around each molecule intersect. Stephens et al. (2006) extend the model to a randomly moving animal encountering a transect, and Rowcliffe et al. (2008) consider a randomly moving animal encountering a wedge-shaped zone of detection for a camera trap. Here we follow Hutchinson and Waser's (2007) and Rowcliffe et al.'s (2008) descriptions of Random Encounter Models (REMs). Assume particles moving in a space of area A, the area covered by a particle is defined by the diameter of the particle (y_i) and the total distance moved

in a given time (d_i) for i = 1, 2, ..., M particles. The expected number of collisions E(C) per unit time is the ratio

$$E(C) = \sum_{i=1}^{M} \frac{y_i d_i}{A} \tag{26}$$

For a stationary object with a circular detection zone or radius r, the area covered by moving animals attempting to encounter the stationary object is the product of speed (v), time (t), twice the radius of the detection zone (r), and the number of particles present given by density x area (DA). Note that we have changed from particle specific velocity (d_i) to an average velocity (v) for all particles for convenience:

$$E(C) = \frac{2rtvDA}{A} = 2rtvD \tag{27}$$

Rowcliffe et al. (2008) modify characteristics of the travel path and detection zone (a pie-shaped segment of radius r and angle Θ). The expected number of contacts between animals and camera traps is given by:

$$E(C) = \frac{2+\Theta}{\pi} rtvD \tag{28}$$

which can be rearranged to give the density as a function of the trapping rate or encounter rate. Let E(C) = y and

$$D = \frac{y}{t} \frac{\pi}{vr(2+\Theta)} \tag{29}$$

By setting Θ = 0, we get the Formoroz-Malyshev-Pereleshin formula (FMP) described by Stephens et al. (2006) for estimating density from the rate of contact between animal tracks and line transects.

This model was evaluated for track surveys by Stephens et al. (2006) using simulations and for Sitka, red, and roe deer. Simulation results showed that low density and low survey efforts were associated with low precision (as is true for all of the models we have presented). With sufficient density and effort, the method produced confidence intervals within 82.5% to 117.5% of true density. In areas of mixed densities, stratification by areas supporting different densities should improve results. Rowcliffe et al. (2008) tested their model using simulation and a field trial in a 226 ha enclosure housing known size populations of red-necked wallabies (*Macropus rufogriseus*), Chinese water deer (*Hydropotes inermis*), Reeve's muntjac (*Muntiacus reevesi*), and mara (*Dolichotis*). Both the field trial and the simulation support the findings of Stephens et al. (2006) that low density and low sampling effort increase uncertainty in estimates. Diel (a 24-hour period) range estimates of target species will also affect results; animals that are relatively sedentary have less likelihood of contacting a camera trap and require either a longer sampling period or a denser array of camera traps.

Assumptions for use of these models include: 1) animals conform adequately to the model used to describe the detection process; 2) photographs represent independent contacts between animals and camera traps; and 3) the population is closed. The underlying assumption behind the first assumption is that animals behave like ideal particles and move randomly and independently of one another. A second underlying assumption is that animals move independently of the cameras. Foster and Harmsen (2012), Noss et al. (2013), and others have cited these underlying assumptions as unrealistic for jaguars and other species because random placement would result in impossibly low encounters, and may not be appropriate for territorial or social species. Rowcliffe et al. (2013) defended their assumptions, arguing that REMs are not sensitive to nonrandom or non-independent movements of animals. Hutchinson and Waser (2007) give many examples of use of random gas models to model encounters between individuals of territorial species, between individuals seeking mates and between groups of social species. Rowcliffe et al. (2013) also point out that the camera trap placement restrictions ensure representative coverage of the area of interest (not often achieved in jaguar surveys) and are no more restrictive than assumptions about the distribution of transects in DISTANCE sampling (Thomas et al. 2010). The key assumption is that animals move independently in relation to the cameras, which is an assumption in almost all spatial sampling protocols.

There have been few applications of random gas models to estimate density. Yapp (1956) and Skellum (1958) used the encounter rate equation to estimate density in early treatments of line transect surveys, modeling the number of encounters as a function of observer speed, target species speed, and detection distance. Rovero and Marshall (2009) applied Rowcliffe et al. (2008) REMs to estimate forest duiker density with poor success. They attributed the poor performance of camera trap REM to the use of generic, published estimates of velocity for duikers that may have been inappropriate for their study. Zero et al. (2013) compared density results for Grevy's zebra (*Equus grevyi*) using REM, DISTANCE-based estimation, and sight-resight estimation and found that all three methods gave similar results. Importantly, movement data was based on data from the local study population.

Estimation of Density and Trends Using Unreplicated Count Data

Unreplicated count data arise in a variety of situations that derive from an inability to visit a sampling unit on more than one occasion. Aerial survey data are often collected as counts on fixed width transects under assumptions of complete detectability (Kinnaird et al. 2012*a*, *b*). Fishery trawl survey data (catch per unit effort (CPUE) data) is often not replicated (Harley et al. 2001), nor are surveys of bat roosts (Ingersoll et al. 2013). North American Breeding Bird Survey is a classic example of surveys based on unreplicated count data at the point level (Link and Sauer 1997, 1998, Link and Barker 2010).

Most survey data for birds and mammals are zero-inflated, meaning that there are more zero observations than would be expected based on a Poisson, negative binomial, uniform, or some other distribution. It is useful to distinguish between kinds of zeroes (Martin et al. 2005). True or

structural zeros arise when the species does not occur at the site either because the habitat is unsuitable or the species does not saturate its suitable habitat by chance. False or sampling zeroes arise due to imperfect detection, temporary emigration, or poor sampling design. Finally, there are the "naughty naughts" (Zuur et al. 2009) or zeros that occur because we are sampling where the species cannot be expected to occur.

Surveys based on unreplicated count data usually rely on strict standardization of data collection protocols (Norton-Griffiths 1978, Robbins et al. 1986) and attempt to control for observer effects in the analysis (Link and Sauer 1997) in order to maintain a constant average detection probability over time and minimize false zeros. Link and Sauer (1998) make the point that use of uncorrected count data as indices requires a careful evaluation of assumptions. They propose models of the form $\log(\mu_{ij}) = \gamma_{j(i)} + \delta_i(t_i) + h_i(t_i)$ where μ_{ij} is the expected count on sample unit (route) i in year j, $\gamma_{j(i)}$ represents the observer effects, $\delta_i(t)$ represents time-related nuisance parameters that affect counts but are not related to population size, and $h_i(t)$ is log of the population trajectory. These individual "route regressions" are then combined using weighted averages to generate trends at larger scales.

More recent approaches to analyzing count data have used hierarchical models (Link and Sauer 2002, Zuur et al. 2009, Kinnaird et al. 2012*b*) to model unreplicated count data. Counts can be modeled using many different distributions, including binomial, Poisson, negative binomial, zero-truncated distributions, zero-inflated distributions, zero augmented distributions, and many more. The choice of a statistical distribution used to model a distribution of observed counts is necessarily subjective, but is guided by careful evaluation of the data. Are the data over-dispersed? Are the data zero-inflated? As we have seen, many of the density estimation procedures use variations of these count distribution models.

Because the "typical" ecological surveys with count data tend to be zero-inflated, we will focus briefly on analytical techniques for zero-inflated data using mixture and two-part models. In both kinds of models, as in the data augmentation models discussed previously, the goal is to model the zero and non-zero count data. In a two-part model (also called a hurdle model), we assume the zero data includes true and false zeros, but do not attempt to discriminate between them. We assume that there are two ecological processes at work; one model governs the absence of a species (a binomial model with covariates and uncertainty about the nature of a zero) and, at the sites where a species is detected, a model governing the number of individuals present. We consider the data (y_i = 0, >0) as a binomial distribution, to model the absence and presence of the species, and then apply a zero-truncated model (Poisson or negative binomial) to model the non-zero counts:

$$f_{Hurdle}(y_i|\beta,\gamma) = \begin{cases} f_{binomial}(y_i=0|\,\gamma) = \pi_i & \text{for } y_i = 0 \\ \end{cases} \qquad (30)$$

$$(1 - \pi_i) \text{ x } \frac{f_{Poisson}(y_i>0|\beta)}{1-f_{Poisson}(y_i=0|\beta)} \qquad \text{for } y_i > 0$$

So the probability of measuring a 0 is π_i and the probability of measuring at least 1 individual is $1 - \pi_i$. π_i is measured as a function of covariates and regression parameters γ. The Poisson count process excludes the zero observations, and the mean is modeled with covariates and regression parameters β. These models can be scaled to the survey area using an offset variable to yield density estimates.

Zero-inflated mixture models also treat the data as coming from two separate processes: the binomial process and the count process. A binomial model with covariates is used to model the probability of measuring a zero as outlined above and a Poisson or negative binomial model with covariates is used to model the counts. The difference between mixture and hurdle models is that the count process can also produce zeros. The count process models the true zeros and the binomial process models the false zeros. So under a mixture model:

$$f_{mixture}(y_i|\beta,\gamma) = \begin{cases} f_{binomial}(y_i=0|\,\gamma) = \pi_{i,false} + (1 - \pi_{i,false}) \text{ x } f_{Poisson}(y_i=0|\beta) & \text{for } y_i = 0 \\ (1 - \pi_{i,false}) \text{ x } f_{Poisson}(y_i>0|\beta) & \text{for } y_i > 0 \end{cases} \tag{31}$$

where $\pi_{i,false}$ is the probability of observing a false zero. Since the binomial is developed in terms of the detection of a false 0, the probability of not detecting a false zero splits the Poisson count process into the probability of a true zero and the probabilities of values greater than 0.

Relative Abundance Indices

Often situations arise where the development of a study to estimate density, occurrence, or abundance incorporating uncertain detection is not feasible. This may be because the design and sampling generated insufficient data, assumptions for analytical models were not met, or the goal of the study did not require unbiased density or occurrence estimates. In these situations, count statistics are often used as indices of relative abundance, or relative abundance indices (RAIs: O'Brien (2011)), under the assumption that detection probability is constant and, therefore, counts of animals or sign vary directly with population size (Caughley 1977).

Indices such as track counts and encounter rates are often used when the target species is difficult to observe directly, determination of detection probability is difficult, or there is the power of historical precedence behind the use of an index. The challenge of sustainable monitoring over vast areas often generates interest in less costly indices, which, because they appear simple, presumably are cost effective and sustainable over time. Even when intended to serve as coarse, large-scale indicators, their appeal needs to be tempered by several caveats and cautions.

Relative abundance indices rely on standardization of environmental conditions, observer skills, survey effort, and execution of sampling to control for factors that might affect detection. The

quality of the survey is completely dependent on controlling the observation process and the nuisance environmental parameters (Link and Sauer 1997, 1998).

However, most relative abundance surveys rely on untested assumptions about the relationship between the index and true abundance, and assumptions about stabilizing detectability through standardization. In practice, standardization of methods is rarely sufficient to control for all possible sources of variation in detection (White 2005). Unequal detectability between counts can generate erroneous conclusions regarding population trends. The use of indices requires the demonstration of a functional relationship between the index and abundance over the desired range of inference, and an evaluation of the precision of the relationship. The assumption that the index has a monotonic relationship with abundance needs to be confirmed (O'Brien 2011, Kinnaird and O'Brien 2012).

Recently, Sollmann et al. (2013) conducted a simulation study of RAIs based on encounter rates (in this case with camera traps) under varying species densities, home range sizes, and trap configurations. They found that differences in detection between species led to positive biases in RAIs favoring the more common species, species with larger home ranges had higher RAIs due to encounters with more cameras, RAIs were sensitive to trap array design (grid versus roads and trails), and that changes in detection over time obscured population trends based on RAIs. These results contradict the few empirical evaluations showing that camera trap RAIs perform well when compared to independently derived estimates of abundance (O'Brien et al. 2003, Rovero and Marshall 2009, O'Brien and Kinnaird 2011, Kinnaird and O'Brien 2012). Sollmann et al.'s (2013) failure to find any relationships in their simulation may indicate that RAIs do not work under the assumptions of the simulations or that some of the simulation studies may have been flawed in some manner.

Results from random gas models suggest that trapping rates are a function of density and velocity of movement (Hutchinson and Waser 2007). If encounter rates can be assumed to be a function of D and local velocity, then encounter rates may serve as an index for density under assumptions of constant velocity. In the Sollmann et al. (2013) encounter rate simulation, the encounter rate with cameras was assumed to vary while population size and home range size remained constant. This can only arise by changing the velocity of movement for each level of encounter rate. For the home range simulations, they implicitly assumed that velocity increased with home range size to avoid the situation where an individual with a larger home range would be exposed to more cameras but encounter each camera less frequently (i.e., kept encounter rate constant at cameras). In a random gas model with constant velocity, as the area increases, the rate of collision (per fixed object) decreases for a constant population size. The mechanism to achieve the encounter rate and home range simulations requires that velocity changes for each simulation and this may have skewed some of the simulation results.

We also know that detection probability can be a function of local abundance, $p_i = 1 - (1 - r)^{Ni}$ (Royle and Nichols 2003), and that the sum or average of point abundances across sample sites

may be a good estimate of total or average abundance. Point abundance estimates (sum or average) derived from methods of Royle and Nichols (2003) and Royle (2004) should therefore track changes in population abundance or density in an unbiased manner and would therefore make a good abundance index. Finally, as we have seen above, properly analyzed unreplicated count data can give useful trend data.

The use of relative abundance indices continues to be controversial. The primary caution is that perceived trends reflect real population changes, not contrasts in detection based on observers, habitat, weather, or substrates. One appeal of camera traps is that they can be applied in a manner which reduces observer bias to the minutiae of camera placement. Direct monotonic relationships between camera-trap-based RAIs and other measures of abundance have been established in several studies (O'Brien et al. 2003, O'Brien and Kinnaird 2011, Kinnaird and O'Brien 2012) and serve as examples of how to validate indices. Any use of abundance indices should be accompanied by a close examination of how the data are collected and treated, and should clearly state the assumptions that are made and the likelihood that the assumptions are justified. Conducting overlapping yet independent methods is recommended to test assumptions, and validate (or reject) measures.

Power Analysis Fundamentals

Statistical power is the probability of detecting a significant effect or trend, despite "noise" such as natural variation. Statistical power increases as sample size and effect size increase, and as variance decreases. Power analyses evaluate the probability that monitoring will detect a change in the event of authentic change, in relation to the probability that monitoring will detect a change when there is no change, or a type-1 error (α); in other words, power is the capacity to detect real change when it occurs, which is the goal of monitoring.

Gerrodette (1987) stated the detection of a trend has 5 parameters: 1) the number of samples, 2) the rate of change of the quantity being measured, 3) the coefficient of variation, which is a measure of precision, 4) alpha (α), and 5) beta (β) (the probabilities of type-1 and type-2 errors, respectively). The value of any one of these parameters can be estimated if the other 4 are specified. Two programs that can be used for power analysis are MONITOR (http://www.esf.edu/efb/gibbs/monitor/monitor.htm) and TRENDS (http://swfsc.noaa.gov/textblock.aspx?Division=PRD&ParentMenuId=228&id=4740; Gerrodette 1987, 1991), where power is given by 1-β(Hatch 2003).

One tradeoff is that it might be better to detect false change versus missing change. If decline is of paramount importance, tests should be 1-tailed, and α not set too low. An example follows, using track surveys of endangered Siberian tigers. Hayward et al. (2002) evaluated a track survey program that would provide over 80% power to detect declines of 10% with a 20% chance of type-1 errors (α). Hayward et al. (2002) used the program MONITOR, examining the capacity to detect change over 5 years. Standard deviations (natural variation) were calculated on a mean

track index from 15 survey areas. Information from data-in-hand went into these decisions. The authors concluded that power was increased by extending route length (which reduced variance), and that power was increased by increasing numbers of routes (e.g., from 3 to 10). Longer routes resulted in decreased variance and less routes with zero counts. Reducing the sample would not permit detections of declines of 10%.

Hayward et al. (2002) cited Kendall et al. (1992) and Beier and Cunningham (1996) as defending a type-1error rate of 20% as a reasonable compromise in endangered species monitoring. These authors were able to use preexisting data to calculate effort needed to provide over 80% power, to detect a 10% annual decline, with a 20% chance of "false alarms." The above example does not translate directly to camera trapping, but illustrates the value of building and layering foundations rich in data, and the demands that documenting trends with confidence can place on researchers.

Power analysis needs input from similar studies, or pilot studies, to generate prescriptions applicable to the study area and species in question. Using simulations based on other sampling efforts might be valid, if sampling practices and natural conditions are similar for the area as for which the power analysis is being conducted.

The simplest prescription for ascertaining trends is repeated measures in the same locale using methods comparable across the sampling events. This will build the data base, and increase understanding of ecological dynamics and jaguar status, in that area.

Field Techniques Applied to Surveying and Monitoring Jaguars

In the following sections we discuss specific methods of data collection for surveying and monitoring jaguars. We focus on sign, interviews, remote cameras, hair collection, the collection of fecal DNA using scat detection dogs, and telemetry. This entire array of methods is relevant to surveying and monitoring jaguars across the NRU. The following sections draw from the monitoring and jaguar literature, with a particular emphasis on obtaining data useful for drawing reliable conclusions.

<u>Sign</u>

In most settings, jaguars avoid direct contact with humans, and dense vegetation reduces the frequency of direct observations. Sign data has enormous potential in monitoring programs if collected under standardized protocols, and analyzed recognizing the limits of inference which can be drawn. In most cases this data is not assigned to individual cats, which imposes limits on inferences of abundance. However, sign is a very valid indicator of presence in an area or specific habitat. Sampling for sign data can be designed for cost-effective contemporary occupancy analyses (Hines et al. 2010, Karanth et al. 2011a, Zeller at al. 2011).

Reading evidence left by wild animals is part of any survey and monitoring effort. Considerable effort may be required for small returns in data, depending on the conditions. The low density and soft paws of jaguars mean that in certain areas (e.g., where leaf litter is dense, or substrates are hard), the jaguar data generated from tracks will be scarce; in contrast, camera traps may yield far more data. Yet, where conditions are favorable, tracks can reveal a great deal, even down to the individual level, for the discerning eye with experience in an area. Used with caution and when combined with other methods, sign surveys represent cost-effective measures of presence-absence.

Recent design and analysis advancements (e.g., De Angelo et al. 2010, Hines et al. 2010, Karanth et al. 2011) bring improved quality control, conceptual frameworks, and models to productively use sign as a coarse measure of area occupied, and thus now provide a useful measure of population expansions or reductions. Eisenberg et al. (1970) qualified the use of indirect methods (tracks and scats) to assess wildlife abundance with comments about track bias due to variation in substrates and scat bias due to decay rates. Multivariate analyses of tracks can help identify species and individuals, but, overall, using tracks to determine animal abundance is challenging with risk for errors. The same applies for accurate identification of scats, which require either strong field evidence as to species of origin, or rigorous analyses to confirm the same. Scats have always provided information about diet. Now, through genetic analyses, they can also provide information about movements, density, connectivity between populations, and even gender and relatedness (Culver et al. 2010). When used within a rigorous framework, sign can be an important tool in registering occupancy and spatial trends.

Tracks

As noted above, tracks are a type of field sign widely used to gather information on animals, including jaguars. In this section we review: 1) resources (books and brochures); 2) the identification of tracks and collection of track data; 3) the type of information that can be learned from tracks, as well as the limitations of inferences; and 4) analyses of track data. Visual guides for identifying jaguar tracks are provided in Murie (1974), Emmons (1990), Aranda (2000), Carrillo et al. (2002), Cuellar and Noss (2003), De Angelo et al. (2008), and Reid (2009). Illustrations can be found in Crawshaw (1992) and photographs in Hoogesteijn and Mondolfi (1992). One of the more complete sets of guidance through drawings and photographs can be found in *Tracking the Felids of the Borderlands* (Childs 1998). Because discerning the identity of cattle-depredating species (dog, coyote, puma, jaguar) is important, virtually every guide to managing human-jaguar conflicts focused on reducing livestock attacks has helpful sketches and guidance for discerning tracks. These guides range from simple folders and brochures through polished presentations available on the web, such as Marchini et al. (2010) and Hoogesteijn and Hoogesteijn (2011) and material on the WCS Guatemala web site (http://www.wcsguatemala.org/en-us/wildlife/jaguar.aspx).

Although tracks can provide a great deal of information, there are a number of risks and limitations associated with track information collection and use. Below we discuss some of those risks and limitations, as well as suggested ways to reduce risks and improve data collection. Jaguar track identification is difficult in many cases, and practice in the field is essential to be able to discern front and rear paw marks, distortions caused by different substrates, and the range of puma tracks from jaguar tracks, especially where sizes overlap.

In the field the most difficult tracks to distinguish are in a mid-sized range, where jaguars and pumas overlap. Mid-sized rear paws lack the extreme breadth of pad and rounded toes so characteristic of a large male jaguar front foot track. While some ideal conditions provide easy visual classification, in less-than-ideal conditions even experts occasionally make mistakes. Sometimes a series of tracks is needed, not just a single one. The following considerations can help minimize substrate-based variation and feature exaggerations that can lead to misidentification of species: 1) consider only flat terrain, 2) avoid identification of tracks on mud or steep terrain, and 3) consider sets of tracks when making identifications (Rosas-Rosas and Bender 2012). Tracks in soft mud and sandy soil can be readily discernible, but with potential distortions due to the soft substrate. Sometimes the best tracks are those in fine morning dust on relatively hard dirt roads on flat terrain that allow identification of diagnostic characteristics (Rosas-Rosas and Bender 2012).

Miller (2001) organized a series of jaguar track collection protocols in the search for low-cost monitoring methods. These included guidance for measuring, tracing, photographing, and identifying tracks. Miller (2001) also performed discriminate function analyses, resulting in 97.2% discrimination to the individual level using 16 sets of tracks (groups of tracks made by the same individual) of 109 tracks and 46 variables.

Recognizing the potentials for using tracks in felid monitoring, De Angelo et al. (2010) applied a dissection of parameters that distinguish jaguar from puma tracks using qualitative traits used by experts to distinguish the 2 species, the level of error associated with these traits, and compared the level of error associated with these traits to multivariate discriminant function analyses. Tracks were collected from 28 jaguars (including 27 adults and 1 juvenile), 29 pumas (including 27 adults and 2 juveniles), 8 maned wolves (*Chrysocyon brachyurus*), and 35 domestic dogs. Because more than one track was collected from some individuals, there were a total of 167 tracks from which the authors could draw random subsets to test. In order to evaluate the accuracy of traditional track identification, the authors conducted a classification exercise with 67 participants from 3 countries, reviewing traditional qualitative differentiation characters, then randomly selecting 10 photographs of tracks from each group and asking participants to classify the tracks. Their performance was compared to 67 random classifications. Volunteers correctly classified 61.5% of tracks. This was higher than the random classification rate of 35%, but nobody correctly classified all tracks, accuracy ranged from 37-87%, and, although 67% of tracks were correctly identified by >50% of the participants, 10 hard-to-identify tracks were incorrectly identified by >50% of the volunteers. This clearly leaves some margins of error, with

rear tracks being the most problematic to identify. The discriminant models achieved an accuracy greater than or equal to 95% in independent track classification. All models misclassified at least one track in cross-validation, and even in some cases in reclassification. In summary, all models achieved 93.5-100% correct classification.

It should be noted that quantitative proportions of tracks presented as useful for classifications in the literature varied widely in performance with the tests conducted by De Angelo et al. (2010). Heel pad:track area ratio showed better results for distinguishing rear tracks in classifications. A more detailed analysis using more tracks from each individual and a wide range of male and female front and hind feet might improve the models the authors developed even further. The take home point is that accurately identifying tracks is not always possible without rigorous cross-checking, and possibly even then errors can be made in identification.

Tracks have an appeal as a low-technology, low-cost index to real abundance. There are, however, caveats to consider. Track encounter rates are strongly related to substrates (J. Polisar, personal observation). In deep forest leaf litter in the Selva Maya of Mesoamerica, jaguar tracks are rare. The same applies to hard clay and gravel slopes on steep slopes. During the dry season in the flat plains of north-central Venezuela, track frequencies can be high in dry season dust on dirt roads, and in daily fresh mud generated as water levels recede across the entire biome. Highly visible tracks can be left in soft soils in forests during the wet season, yet may be obscured by the next deluge. Track sign is not only affected by variation in weather, substrates, and observers, but also intra-specific and inter-site variability in jaguar movement patterns. Conde et al. (2010) documented differences in habitat preferences and travel routes between females and males in southeastern Mexico, resulting in variation in track encounter rates between female and male jaguars within the study area.

Shaw et al. (2007) provided relevant written and visual guidance on identifying puma tracks and advice on using sign surveys. Important considerations include matching objectives to methods, and standardized selection of route location and length, data collection, and observer capacity. Smallwood and Fitzhugh (1995) surveyed the state of California for puma tracks (and trends) using 3-km transects on dusty dirt roads from 1985 to 1992. For their study, dust ratings were required at the beginning, middle, and end of each transect, and all units of effort and measurement were standardized. The effort was coordinated as tightly as its scale allowed and viewed as an index, with the understanding that some sampling noise was unavoidable. Beier and Cunningham (1996) surveyed dry washes in Arizona and estimated the effort required to detect changes in a puma population, using field data and simulations to conduct power analyses. They concluded that: 1) based on labor-scale constraints, track surveys could detect relatively large changes in puma population size (an enormous sample was required to detect fine changes); and 2) considerable sampling was required to detect even coarse changes, but the method could yield relatively cost-effective indices that could be easily replicated and standardized among observers, with 80% power a reasonable goal. This conclusion might be challenged when working with extremely low-density populations and scarce individuals, but coordinated and

standardized sign surveys, taken as the indices that they are, have the potential to provide valuable, if crude, measures of trends and relative abundance in occupied areas.

Polisar et al. (2008) augmented data from telemetry and camera traps to draw inferences about jaguar and puma habitat preferences based on sign frequencies collected using standardized data collection protocols in a habitat-stratified system of 28-linear-foot transects. With the caution that soft substrates were productive for track deposition, but hard soils and rocky substrates less so, the subtle contrasts in track frequencies among habitats coincided with telemetry-based analyses of habitat preferences (Scognamillo et al. 2003) and camera trap photograph frequencies (Polisar 2000).

Balme et al. (2009*a*) used a complete count of radio-collared leopards to evaluate efficacy of track counts and camera traps as estimators of abundance and density. In their study, track identity was confirmed by locations of radio-collared animals on 23 occasions after intensively following tracks (and collared animals). The study used standardized methods (transect routes, times, speed) restricted to areas with suitable substrate, with the observer being a skilled tracker seated on the front of the vehicle. Since abundance/density was the goal of this calibration exercise, tracks that could not be identified were excluded from analyses. The researchers plotted track density and frequency against effort to determine the sampling effort (km driven) at which the coefficient of variation reached an asymptote and increased effort was not justified. They discovered that male leopard tracks were found on roads more than expected, as well as that all analytical methods used to estimate density from tracks had shortcomings, with the best estimate coming from a rigorous capture-recapture framework; however, even this estimate was out-performed by camera traps. The authors note how changes in substrates may introduce bias. For example, soils in less frequented area may be better for track deposition than soils in an area where the abundance and activity of the study animals may actually be higher. Behavioral differences in gender may also have introduced bias; male leopards used roads more frequently than females (Balme et al. 2009). Most carnivore studies will lack similar capacity to reliably assign identity to tracks, particularly if studies are multi-observer and large scale.

The authors conclude that track counts are less expensive to implement than camera-trap surveys and easier to implement over a large area, but accuracy levels to estimate population numbers are poor. Track counts may, however, be satisfactory when the objective is to gauge trends in abundance over time (i.e., an index to abundance over time). The authors recommend: 1) caution when using relative abundance indices to make comparisons over space and time, and 2) calibrating the track count index with at least one other independent abundance estimate technique. They state that the poor performance of track counts limit wide applicability, except in ideal circumstances where they may be suitable for monitoring trends in abundance at the same site over time.

If tracks are used as a measure of spatial or temporal population trends, it is critical that as many sources of variation be reduced as possible and standardization is required. The results will have

more utility within biomes and study areas as coarse measures of spatial trends, with too many caveats to be considered reliable measures of numerical trends.

Scrapes

Scrapes were the most common sign encountered on trails in the Cockscomb Basin Wildlife Sanctuary in Belize; therefore, Harmsen et al. (2010) examined them in conjunction with scat and camera trap surveys. Scrape surveys were conducted along old logging roads with no vehicular traffic. Camera stations were spaced at ~ 1km intervals along survey trails, located to optimize capture probability of jaguars and pumas. Scats were collected during the systematic scrape survey, and genotyped to species (Foster et al. 2010b). A scrape was recognizable as raked ground with loose earth piled up at one end. Two types of scrapes were observed, either two parallel rakings separated by a ridge of loose soil (double scrape) or single rakings with no partition (double scrape). Scats genotyped as jaguar and puma were found in scrapes and camera and video traps recorded both species in the act of scraping. Single scrapes were made with a front foot, and double scrapes were made with both hind feet.

There was no morphological feature that allowed attribution of a scrape to either species with certainty. Genetic data from scats was needed to identify scrape to species. Pumas were more likely to scrape with their hind feet and created smaller scrapes than jaguars. At a broad temporal scale (average over 9 weeks), scrape production was related to number of male puma visits (activity), and number of individual male jaguars (abundance). On a weekly scale, scrape production also correlated positively to jaguar and puma traffic, but more so with male puma photo capture rates and less strongly for jaguars, with the more intermittent use of trails by jaguars offered as a possible explanation (Harmsen 2010).

Kills

An important aspect of monitoring jaguars is understanding their prey. In ecological studies on tigers, lions, and jaguars and their prey base (Schaller 1967, 1972, 1983, Karanth and Sunquist 1992, 1995, Polisar et al. 2003, Scognamillo et al. 2003), strong data on prey abundance and biomass has allowed an interpretation of prey selection patterns. Knowledge of food preferences and prey base clarifies an area's capacity to support large cats. Kill records provide ecological information, and along with tracks and scats, constitute valuable presence data for monitoring programs.

In the absence of telemetry, kills can be located by scouting places that are rich in prey, and watching vultures can also help. The closest to a systematic method for locating jaguar kills is using telemetry to identify areas where jaguar movements have become reduced, and then searching the site after the cat has left. With VHF transmitters, one of the positive tradeoffs of needing to be physically near tracked cats to receive a signal and then proceeding to where they had been was that this did not involve much extra effort (Polisar et al. 2003, Scognamillo et al. 2003, Azevedo and Murray 2007*a*, Cavalcanti and Gese 2010). With the increased use of global

positioning telemetry systems using GPS clusters (Knopff et al. 2009, Ruth et al. 2010, Tambling et al. 2010), the potential for locating kills has actually increased because of the ability for continuous monitoring to help discover location clusters that can guide researchers to kills. This elevated efficiency in pinpointing possible kill sites does not diminish the need for actual field visitation to confirm and identify the characteristics of the event (Ruth et al. 2010).

To determine jaguar presence using kills and better understand jaguar diet, it is critical to correctly identify whether an animal was killed by a jaguar or another species, such as puma. Guidance on how to distinguish jaguar and puma kills in livestock attacks is provided in Brown and López-González (2001), Childs (1998), Hoogesteijn and Hoogesteijn (2011), Marchini and Luciano (2009), and at the Wildlife Conservation Society Guatemala website (http://www.wcsguatemala.org/en-us/wildlife/jaguar.aspx). Additionally, jaguar attacks on other prey can be identified by: 1) punctured braincases at the top of the occipital lobe (such as might be found with peccaries); 2) bite marks on back of neck near the base of the skull; 3) bite marks on top of the nose and/or near the eyes; and 4) caiman that are essentially peeled open. Kills demonstrating asphyxiation (punctures in throat) or are covered with debris are generally from pumas. Additionally, when consuming livestock, jaguars tend to initially focus on the front part of the animal, such as the chest, shoulder, and neck, whereas pumas tend to focus on the middle of the animal, usually around the rib cage and vital organs. Kills in which the skull shows substantial punctures in the nucal (external surface of the occipital bone) area and animals with the first vertebrae broken tend to be jaguar kills.

Tracking prey and kills provides a strong data point indicating presence, and can be a rich experience that imparts an intimate understanding of cat behavior. Due to variation in individual jaguar prey selection patterns and kill detectability (cover, access, decay, size of prey), however, these data are not suitable as jaguar population estimators, or even as indications of population trend.

Scats

Jaguar scats can be used to understand diet, as well as identify sex and individual jaguars. There are a number of techniques that can aid in positive identification as jaguar scats. For example, Emmons (1987) restricted her scat-based comparison of food habits of ocelots (*Leopardus pardalis*), pumas, and jaguars in Peru to scats associated with tracks, trapped individuals, radio tagged individuals, or hair ingested while grooming. Taber et al. (1997) used thin layer chromatography to separate bile acids present in 280 scats thought to be large cats in the Paraguayan Chaco, assigning 106 and 95 scats to jaguars and pumas respectively. Nuñez et al. (2000) examined food habits using 50 jaguar and 65 puma scats in Jalisco, Mexico, using tracks to determine the species of cat responsible for scats, and excluding scats with no accompanying sign from the analysis. Azevedo and Murray (2007) used the same exclusion principles (no confident sign accompanied with the scat = no species identification) for their study.

Identification of scats can be confirmed with DNA analysis (Heinemeyer et al. 2008). Farrell et al. (2000) developed primers that targeted mitochondrial DNA cytochrome b gene to analyze 34 scats (of 70 collected in the field), with 20 successfully amplified and sequenced to species (jaguar, puma, ocelot, crab eating fox (*Cerdocyon thous*)) up to 3 years after collection, allowing confident assignation of prey species in scats to species of carnivore. These methods were repeated and amplified in Scognamillo et al. (2003) with 42 scats each from jaguars and pumas, which, together with VHF tracked kills, allowed analyses of diet overlap and differences between the two species, and an understanding of prey selection patterns by both large cats (Polisar et al. 2003). Without genetic identifications, confident assignation of the origin of the majority of the scats would have been impossible.

Building on the work of Farrell et al. (2000), Hang et al. (2009) developed and tested a method for DNA-based identification of jaguar and puma scat samples. The molecular approach was developed using 52 reference samples from throughout the jaguar's range, including blood, tissue, hair, and scat. In addition to those samples from known specimens, they analyzed 55 scats collected by researchers from different parts of the Brazil-Argentine Atlantic Forest and identified as large felid based on morphological features (shape, size, diameter), as well as tracks. Thirty-four of 39 fresh scats from captive jaguars were successfully amplified and sequenced, with more variable success rates from scats collected in the field, likely due to diverse environmental conditions, sample age, storage time, and storage method. For example, from Misiones Province of Argentina, scats with the field assigned label of "fresh" had an 89% success rate, while those labeled "intermediate" had a 59% success rate. Scats labeled "low quality" in the field had a 14% success rate. Murphy et al. (2007) found that time-in-field, temperature, and moisture affected mitochondrial and nuclear DNA amplification success with brown bear (*Ursus arctos*) scats, with the greatest success occurring between 1 and 3 days (of scat age). Of 21sequenced samples from Misiones Province, 18 were identified as jaguar or puma, and another 3 as ocelot despite their original "large felid classification." Foster et al. (2010) opportunistically collected 645 scats in southern Belize. The genetic identifications for 532 of these scats were 362 jaguars, 135 pumas, 33 ocelots and margays, and 2 domestic dogs. Without genetic methods, jaguar and puma scats would be far less distinguishable—a factor to consider if using scat frequency as an index of jaguar trends and when examining jaguar diet.

Michalski et al. (2011) successfully identified eight carnivore species from 71% of a sample of 93 scat samples from the southern Brazilian Amazon. The researchers collected 109 carnivore scat samples within 13 months through 690 km on foot, and another 153.8 km surveyed with a trained scat dog. The locations of all scats were geo-referenced. At the moment of collection, scats were subjectively classified to four condition categories based upon odor and three subjective moisture categories. Sixteen scats were excluded from molecular trials due to deterioration from rain and insects. Team leaders were always present to control scat condition scores. Species identification was performed using a short fragment of mitochondrial DNA following methodology described in Haag et al. (2009). Among factors affecting success were

distance to forest edge (scats in open areas were more “weathered and sun-exposed”), season (wet season deteriorated scats faster), and sample condition. Scats with no odor and no moisture (low freshness) had a lower probability of success in the first polymerase chain reaction (PCR) sequence, and number of PCR attempts before a successful sequence was a negative predictor for positive species identification. The number of PCRs required before a successful amplification was strongly negatively related to the age of the scat, with results from the Amazon similar to those Murphy et al. (2007) obtained in Idaho for bears. Exposure to high humidity, warm temperatures, frequent rain, and intense sunlight may degrade DNA (Michalski et al. 2011). Although humidity and insects in forests may degrade DNA, the more intense rainfall and sunlight in open areas represents a greater risk to identifications. The take home message is that scats should be as fresh as possible.

Roques et al. (2011) developed a rapid classification protocol for polymerase chain reactions for the unambiguous identification of scat of sympatric Neotropical felids, which was optimized with samples of known origin, and validated in 138 samples of unknown origin. The authors suggest that this reliable, cost-effective approach with high identification success rates should facilitate its application for surveys of presence-absence and abundance.

In the following section we present advances in identifying scats to the sex of the jaguar they come from and sampling considerations to reduce bias. Palomares et al. (2012) optimized methods developed by Pilgrim et al. (2005) for sex identification of scat. Species and sex was determined for 493 scats collected from six sites in Yucatan, Mexico, and 4, 1, 2, and 1 site respectively in Brazil’s Amazon, Pantanal, Cerrado, and Caatinga, resulting in identifications of 246, 216, and 31 jaguars, pumas, ocelots/margays, respectively. The location of all scats was georeferenced with a GPS. The proportion of male scats was high, with an average of 4.6 scats per male and 2.0 for each female. To the various explanations offered by the authors, we will add that researchers’ travel and sample routes along roads and trails might have selected for male scats, as they more typically use those travel routes. Females are generally more reticent to cross open spaces or use wide paths; thus, the results of this large scale survey echo some results produced by camera traps being opportunistically set in travel routes preferred by males. The detail of analysis is exemplary, and provides another argument that all scat surveys employ genetic identification.

Heinemeyer et al. (2008) discussed survey considerations for natural sign and scats in detail. An extracted interpretation of the conclusions includes the following: 1) despite the temptation to use established trails and roads, doing so exclusively may generate bias, and will certainly cause issues with comparisons unless the sample design is consistent throughout the survey; 2) selective sampling, such as habitat stratification guided by prior knowledge of a species habitat use and travel patterns, can increase efficiency; 3) all parameters of the survey (units of effort and recording procedures) must be pre-determined and consistent; and 4) sign accumulation (old tracks and scats) needs to be considered in survey timing and recording procedures. In addition,

until scats are identified via DNA, their origin is in question. The manual written by Amato et al. (2008) provides guidance for field procedures in collecting and storing scats.

Karanth et al. (2011) conducted landscape-scale tiger sign surveys in India using an occupancy model (rather than comparisons among transects) that Hines et al. (2010) developed, which allowed serial spatial replicates (trail segments) and incorporated prey abundance, human disturbance, and proportion of habitat surveyed. Only unambiguous sign was recorded, and survey teams photographed, geo-referenced, and recorded sign of tigers, leopards, dholes, ungulate prey, and livestock presence. A grid of square cells was superimposed upon a map of the study area, with the 188km² grid cells larger than the average tiger home-range size. Within these cells, each type of sign detection was assigned only once to each 100 m trail segment (yielding the 1 or 0 detection/non-detection history required for occupancy analyses). The sign detection data were aggregated at 1km length to form spatial replicates of 4-40 1km sections per grid cell. Comparisons of probabilities of site occupancy matched well with knowledge about tiger densities obtained using other methods (camera traps). Pending consistent training of observers, tight field coordination, and favorable conditions for sign, this approach has tremendous potential for jaguar occupancy evaluations over large areas.

The preceding section has described the potential pitfalls and benefits of using field sign (tracks, kills, and scats) for monitoring jaguars. Paramount in the use of field sign is accurate identification of all three as coming from jaguars. Obviously, without that confirmation, their value in a monitoring program is dubious. Direct animal observations are usually reliable, but field sign can be ambiguous, which makes adequate training of field staff, standardizing sampling effort, and data quality control and validation all particularly important. Field sign does confirm presence, and can easily be used in presence-absence modeling.

Interviews

Interviews with local informants are a valuable method for gathering information on jaguars, especially on distribution and qualitative trends. An enormous proportion of historical jaguar accounts are attributable to interviews in an informal sense. Brown and López-González (2000, 2001) bring the jaguar of the northern limits of modern jaguar range to life by including rich stories from hunters, which complement the historical records they collected to provide evidence of jaguars in northern Arizona and central New Mexico as late as 1900-1925, and a range limit retraction much farther south 50 years later. Quiroga et al. (2013) augmented camera trap surveys and transects with informal interviews on the contemporary southern edge of jaguar range, finding that despite vast areas of semi-arid dry forest habitat, the jaguar had been eradicated from this area, a situation similar to the southwest region of the United States. This section will bypass the wealth of anecdotes available in historical accounts, such as found in Mondolfi and Hoogesteijn (1982), and will concentrate on recent efforts to establish jaguar distribution and trends using interviews.

McNab and Polisar (2002) describe interviews used to rapidly appraise the distribution and status of jaguars in Guatemala. In this study, parabiologists from the community of Uaxactún in the heart of the Multiple Use Zone of the Maya Biosphere Reserve played a lead role in an appraisal of jaguars in the 21,000 km² biosphere reserve. A standardized questionnaire was used to interview protected area personnel, forest extractionists, and hunters. Participants were asked about records of jaguars, methods of identification, presence of prey, and value of the site. The data were organized into four categories on a gradient of reliability: 1) direct encounter with jaguar by observer; 2) sign detected by observer; 3) second party to a direct encounter; and 4) second party to an encounter with sign. Wildlife Conservation Society, Guatemala personnel headed interviews outside the reserve, on a national level, using the same questionnaire. The results were a rapid and inexpensive assessment of jaguar distribution throughout the entire country. The Uaxactún parabiologists had high interview success, with respondents feeling more comfortable to disclose information to them than they would with "outsiders."

Figel et al. (2011) worked with Chinantec communities in a rugged, remote rainforest region in southwestern Mexico by combining interviews and camera trap surveys to evaluate jaguar presence recording 103 visual sightings of jaguars by 67 individuals, with 83 sightings since 1990, and 60 since 1999. Laminated sheets with photographs of native and non-native prey and carnivores were used to assess wildlife knowledge and the veracity of observations. While a measure of public perceptions of jaguars was an underlying goal in the interviews, they also helped elucidate distribution of jaguars within the area.

Between 2002-2008, De Angelo et al. (2011) conducted 70 training workshops on sampling techniques and data collection with people working and living where large carnivores were potentially present in a tri-national (Argentina, Brazil, Paraguay) area in the Upper Paraná Atlantic Forest Region. Starting with park rangers, field biologists, and members of governmental and non-governmental organizations, their network of volunteers expanded to include farmers, ranchers, forest workers, army personnel, and students. They trained participants to search for and collect track imprints and scats of large carnivores.

Collaborators in this study were provided a kit with supplies for making plaster molds of tracks and collecting and storing scat samples. These kits included field guides, prepared data cards to fill out, disposable gloves, silica gel, questionnaires, and all of the materials needed to collect physical evidence of large carnivores, record associated data, and store samples for confirmation. Although data collection was by volunteers, species confirmations and data analyses were conducted by professionals. The protocol established by De Angelo et al. (2010) was used to identify tracks, and the methods developed by Haag et al. (2009) were used for DNA identification of species. Local people participated in study design and data collection. Data analysis and decisions were made by professionals. The standards for assigning species identification were relatively high (discriminant function analyses of tracks, DNA identifications from extracted scat material).

A total of 320 people representing 40 institutions were trained. Participation was dynamic but at least 100 people participated in the entire six year monitoring period. The collaborative effort resulted in 2,667 records whose distribution covered 92,890km², although most of the data were concentrated in 54,181km². Records of pumas were more abundant, while records of jaguars were more concentrated in the largest forest fragments, often associated with protected areas.

Zeller et al. (2011) integrated interview data and occupancy modeling to identify a jaguar corridor in Nicaragua. Corridors in this area are in human-dominated landscapes and are large in scale, making intensive techniques such as camera traps or transects economically infeasible. On the other hand, occupancy surveys based on interviews with local people, while relying on the credibility of local observers and quality of data collected by the interviewer (which entails risks in accuracy), seem to balance the possibility of covering large areas with low costs.

Zeller et al. (2011) divided their Nicaragua study area into 6 x 6 km² sampling units, with size based on estimated jaguar home range, which resulted in 71 such units covering a total of 2,556 km². They developed questionnaires identifying each participant's area of knowledge and treated each interview as a separate replicate to compute detection probabilities, conducting four to six interviews per sampling unit. Questionnaires were designed to gather detection/non-detection data on jaguar and seven prey species. The criteria were that the interviewee had either lived in or visited the sampling unit at least twice per month in the preceding year. Interviews were used to generate within-unit detection probabilities via spatial replication, within the time frame of a year. Detection was qualified as direct sighting, direct observation of sign, or direct observation of a jaguar kill (Zeller et al. 2011).

Zeller et al. (2011) did not collect track molds or scats when testing the feasibility of interview-based occupancy surveys in a corridor area (areas connecting protected areas/source sites) in Nicaragua. However, interviewees were vetted through a two-step process, first asking them to describe the animals being discussed (jaguar or prey), and then asking them to identify the animal and its tracks from a menu of pictures. In addition, researchers made it clear that all information provided would be anonymous. Because the study incorporated data based on an interval of one year and assumptions of independence, the results were not "true occupancy," but rather "proportion of area (of total sample) used," an acceptable constraint for a corridor area. Given the goal of identifying the use of a corridor (intended to provide a travel area connecting source sites), this was adequate. Covariates included a series of habitat characteristics (proportions of forest, grassland, agriculture/shrub, open areas, early stage secondary forest, wetlands, and water), as well as mean elevation and distance to protected areas (Zeller et al. 2011).

Given the error rates, De Angelo et al. (2010) observed among experts in distinguishing jaguar and puma tracks the accuracy of the interviews might not be high, but this approach covered a vast area of low jaguar density with minimal costs. This is a protocol that could be used within corridors, and perhaps at the margins of core populations, but not within core areas. Areas where

human population density is low and jaguar density is higher are better suited for sign-based occupancy surveys (substrate and terrain depending) or capture-recapture methods, or a mix of the two based on a gradient from edge to core.

Interview-based occupancy surveys have the utility to assess observations of jaguars and their prey in recent time on a large spatial scale. Using rigorous questionnaire procedures, treating each observer's knowledge as an observation, and achieving replicates through multiple observers, probabilities of detection can be assigned within each sampling cell and related to covariates, to provide distribution information for jaguars and their prey. Given that monitoring must seek to keep a number of factors constant in order to discern trends, likely observer variation in this volunteer-based method with no field confirmation requires that it be limited to large-scale, non-core areas if used as a monitoring tool. It should be complemented by overlapping sign validations where feasible. If jaguar densities are really low, and potential interviewees few or unlikely to divulge information, then expert driven searches into areas where jaguars are likely to occur may be more reliable, whether sign-based, image-based, or both.

Remote Cameras

The first remote cameras designed to photograph wildlife (also known today as camera traps or game cameras) were developed shortly after the invention of flash photography in 1899 (Guggisberg 1977). A few zoologists explored the scientific potential of remote cameras throughout the early and mid-20th century; however, limitations related to cost, time, and effort left generations of scientists and land managers to view the tool as impractical (Kays and Slauson 2008). Adoption of the technology by deer hunters in the late 1980s to scout potential hunting grounds left manufactures scrambling to meet this new demand and explore technological advances. Biologists began adopting the rapidly improving technology *en masse*, recognizing the value of a permanent record of observed animals and the potential of applying remote camera data to statistical tools developed for other survey methods. Remote cameras provide a non-invasive method for detecting rare, shy, and cryptic species, as well as for identifying species that cannot easily be distinguished from tracks or other sign.

Kays and Slauson (2008) accurately reflected on three main objectives of early scientific publications accomplished with remote cameras,

> …*1) detecting the presence of a species* (Kucera et al. 1995, Foresman and Pearson 1998), *2) estimating animal abundance* (Mace et al. 1994, Karanth 1995, Jacobson et al. 1997, Karanth and Nichols 1998), *and 3) recording animal behavior* (Carthew and Slater 1991, Bull et al. 1992, Vanschaik and Griffiths 1996).

Extending beyond these early efforts, biologists currently use remote cameras to determine occurrence or presence and distribution, relative abundance, abundance and density, and to monitor the abundance and distribution of species over time. Perhaps the most novel application

of camera traps has been to generate information on abundance and population density, in particular applying capture-recapture analytical methods (Cutler and Swann 1999, O'Connell et al. 2011).

Pioneers of many of the methods discussed here include Karanth (1995), Karanth and Nichols (1998), Karanth et al. (2004, 2011*b*, *c*), Simcharoen et al. (2007), Royle et al. (2009*a*, *b*), and Gopalaswamy et al. (2012*a*) through their work on Asian tigers. Others who have developed many of the methodologies include O'Brien et al. (2003), Kawanishi and Sunquist (2004), Wegge et al. (2004), Johnson et al. (2006), Harihar et al. (2009), Lynam et al. (2009), Wang and Macdonald (2009), and Sharma et al. (2010). These methodologies have been subsequently applied to estimate abundance of other felids whose markings permit individual identifications, including leopards (Henschel and Ray 2003, Ngoprasert et al. 2007, Balme et al. 2009*a*, Wang and Macdonald 2009, Chapman and Balme 2010), snow leopards (Jackson et al. 2006, McCarthy et al. 2008, Janečka et al. 2011), cheetahs (*Acinonyx jubatus*; Marnewick et al. 2008), and ocelots (Trolle and Kery 2003; Maffei et al. 2005; Trolle and Kéry 2005; di Bitetti et al. 2006, 2008; Dillon and Kelly 2007, 2008; Kolowski and Alonso 2010; Diaz-Pulido and Payán Garrido 2011).

Jaguars have been the subject of many camera trapping studies (Maffei et al. 2002, 2004; Maffei et al. 2011a; Wallace et al. 2003; Kelly 2003; Silver et al. 2004; Cullen Jr et al. 2005; Soisalo and Cavalcanti 2006; Ceballos et al. 2007; Salom-Pérez et al. 2007; Paviolo et al. 2008; Silveira et al. 2010; de la Torre and Medellin 2011) extending from the species' northernmost limits in Arizona to its current southern bounds in northern Argentina.

The extent of jaguar range currently occupied (~61% of the species' historical range), large size of JCUs (e.g., 25,000-100,000 km^2) (see Sanderson et al. 2002, Zeller 2007), low human population densities in comparison to India, and correspondingly less transportation infrastructure, has meant that camera-trapping for jaguars occurred in quite different environments than where camera-trapping has been conducted on tigers. Some jaguar habitats provide very challenging access logistics, which, in the past, have influenced study design. Jaguar study areas can range from vehicle accessible areas to places requiring three to five days river travel in dugout canoes to simply reach the study site. Yet, proceeding forward, the principles of study design and data analysis remain the same no matter the logistical challenges or biome, whether it is xeric (arid) or wet.

A paper by Silver et al. (2004) and manual by Silver (2004) informed a generation of jaguar camera trappers. Since then, camera trap technology has advanced, new analytical models have become available, and experience has informed camera trap users on how efforts at jaguar population estimation can be improved.

The objective of a mark-recapture (or photograph/re-photograph) study is to estimate the number of individuals within a sample area. In basic terms, this estimate is generated by first estimating capture probability based on the capture histories of animals photographed. The number of

animals in the sampled area is then estimated by dividing the total number of animals "caught" by the estimated probability of catching an animal at least once. The technique does not have to be based on a non-random sampling of the area, i.e., the cameras are set up in a pattern designed to maximize capture probability for all animals in the sampled area. The more individuals of the target species that are photographed, and the more often each individual can be photographed, the more robust the resulting abundance estimate.

When White et al. (1982) developed the method for small mammals, they recommended a minimum of 75-100 individuals, 20 recaptures, and a capture probability of 0.30. In camera-trap surveys for jaguars, between 2 and 27 individuals have been identified, but most surveys have recorded less than 10 individuals. The number of individuals can be increased by enlarging the camera trap polygon, but the upper limits of this expansion can be constrained by logistics and costs, which mean that detecting 75-100 individuals is impossible in practical terms. Caution is warranted for the density estimates generated by extremely small samples (Maffei et al. 2011*b*). Recent SECR models may more successfully address problems posed by individual heterogeneity in capture probabilities in conventional capture-recapture analyses, offering non-asymptotic inferences more appropriate for small samples of capture data typical of photo-capture studies (Gopalaswamy et al. 2011). However, all capture-recapture estimates will suffer low precision if recaptures are infrequent, and the logistical challenge of obtaining adequate recaptures of animals that roam over large spaces persists for all analytical models.

Reviews of past jaguar surveys and subsequent recommendations for surveys are presented in Maffei et al. (2011*a*, *b*), Foster and Harmsen (2012), Noss et al. (2012), and Tobler and Powell (2013).

It is important to distinguish between: 1) studies that are exploratory in nature assessing the presence of jaguars in an area; 2) studies intended to use data as indices to compare relative abundance across threat levels, habitat types, land use prescriptions, or even time; and 3) studies intended to generate an unbiased and precise (and thus accurate) estimate of jaguar population density in the sample area. The objectives of all three types of studies are legitimate and contribute to the collective knowledge about jaguar distribution and abundance. However, the objective of the third study has a particularly demanding set of requirements to generate a quality estimate. Of the three, the latter requires the most care in preparation, and should not be attempted unless adequate time, resources, and equipment will allow the rigorous sampling needed.

New digital camera traps can operate for lengthy periods with minimal battery draw-down and with considerable storage capacity. For remote areas, with some study areas literally days from the nearest road, this is a huge advance. Criteria to look for in digital cameras include: 1) fast shutter speed both day and night (less blur and better identification of individuals); 2) night flashes that balance illumination with desired range, neither "washing out spots" with too much flash, nor missing identifications of individual cats a bit further out due to inadequate flash; and

3) capacity to take serial photographs with one event—because cats are mobile and identification through spot patterns is the goal, the more photographs from the maximum number of angles possible of that cat at that time, the less missed opportunities for identification. The combination of digital camera traps capable of recording a rapid sequence of photographs and the standardized application of a local attractant (e.g., Calvin Klein's Obsession for Men) can both cause the jaguars to linger in front of the camera, and maximize the opportunities for adequate photographs from multiple angles to identify the individuals (Maffei et al. 2011*b*, Moreira Ramirez et al. 2011, Isasi-Catalá 2012, Noss et al. 2013).

Designing Surveys

Because camera traps are used to collect data on a number of topics, including species diversity, species presence, wildlife use of key resources, habitat use, and activity patterns (Maffei et al. 2002, Arispe 2007), each of these objectives should guide a particular survey design. A good design for one objective will not necessarily be the best design for another. We focus below on systematic camera trap surveys used to estimate population abundance and density by applying capture-recapture analytical methods.

Abundance

For the purpose of abundance estimation, detection probability can be defined as the likelihood that an individual will be detected (photographed or captured) if it is present in a sample unit during the time of the sample. Detection is a source of variability in abundance estimation because not all animals will be detected with absolute certainty during a sampling effort, individuals may vary in their detectability, and detection may vary over time and space. The likelihood of detecting an individual during a sample occasion provides the key to converting the sample count statistic into an estimate of abundance or density. Detection probabilities therefore are an important component of any abundance estimation exercise or monitoring program (O'Brien 2011).

Two critical assumptions need to be satisfied when designing a mark-recapture camera-trap survey. These assumptions are discussed in detail in Karanth and Nichols (1998) and summarized below.

Population closure: The mark-recapture model is based upon a closed population, i.e., no births, deaths, immigration, or emigration of individuals within the study area during the survey (O'Brien 2011). In reality, few jaguar populations are actually closed, so in practice the assumption is satisfied by limiting the duration of the survey. The longer the survey lasts, the greater the likelihood there is of violating this assumption. Based upon the life history characteristics of tigers, Karanth and Nichols (1998) concluded that three months was a reasonable time-frame to assume a closed population. Similarly, surveys on African leopards have typically used two to three months (Henschel and Ray 2003). Numerous jaguar surveys

have used three months or less (Wallace et al. 2003; Maffei et al. 2004, 2011*a*, *b*: Silver et al. 2004) as a data-collection period.

All individuals have non-zero capture probability: The second important assumption is that every individual inhabiting the study area has at least some probability of being photographed (i.e., there is at least one camera trap within its range during the duration of the survey). It is important to realize that not every jaguar in the study area needs to be photographed, but that every animal has some chance of being photographed. This assumption dictates how far apart your camera traps can be placed and determines the maximum size of a contiguous area within the study site without any camera traps. The camera stations can be as close as the researcher is inclined to set them, but there must not be gaps between camera stations large enough to encompass a jaguar home range. A conservative approach to satisfying this assumption is to adopt the smallest home range estimate documented for your target species in your habitat and/or geographic region as the minimum area within which there must be at least one camera station. Once that minimum area is known, calculate the diameter of a circle with that area. This diameter is the maximum allowable straight-line distance between camera stations.

Female home ranges are generally smaller than male home ranges (Rabinowitz and Nottingham 1986, Crawshaw and Quigley 1991, Scognamillo et al. 2003, Cavalcanti and Gese 2009). Initially, recommendations for space between stations were based on an extremely small home range of 10 km² recorded in Belize (Rabinowitz and Nottingham 1986). Despite the validity of that record, drawing from the wider range of estimates of 10-65 km² recorded in Mesoamerica would generate diameters of 3.2-8.1 km (Maffei et al. 2011*b*). Home ranges recorded in South America have tended to be larger, with male ranges frequently over 100 km² (Scognamillo et al. 2003, Cavalcanti and Gese 2009) and sometimes several hundred square kilometers in size (Tobler and Powell 2013). Low density populations demand large sample areas and require wider spacing. In general, wider spacing will allow more animals to be caught, facilitate a larger sampling area, and is therefore encouraged. The caveat is that females that have recently given birth and are with small cubs use small areas (Farrell 1999), which expand with time.

The tension between sampling a huge area with widely spaced camera trap stations, and spacing stations close enough to maintain the probability of all animals being captured at >0, means that studies must aim for a compromise. Sollmann et al. (2011) deployed a grid with maximum distances of 3.5 km between stations in an area of extremely low densities in Brazil, while Tobler and Powell (2013) suggested spacing as wide as 4 or 5 km based on circular home ranges of 50 and 80 km², the former of which appears to be a biologically reasonable maximum based on female home ranges in Venezuela and Brazil (Crawshaw and Quigley 1991, Scognamillo et al. 2003, Cavalcanti and Gese 2009).

It is acceptable to miss some individuals, as analytical methods are based on detection probability, but each individual should have some possibility of being captured. The requirement of non-zero probabilities of capture have relaxed with the advent of maximum-likelihood and

Bayesian SECR approaches that model detection processes through the distribution of home range centers. The maximum likelihood method assumes that the probability of capture of an animal at a distance *d* from its assumed home range center, follows a two parameter spatial detection function *g(d)* and spatial scale parameter σ related to home range width (O'Brien and Kinnaird 2011). Efford et al. (2005) pointed out that the distances between sampling points should be on the scale of animal home ranges in order to sample movements. Sampling designs which adequately provide opportunities for residents to be captured and have the extent of their movements recorded remain sensible, even with SECR.

Planning the Survey Area and Duration

While there is no set minimum distance between stations, a survey will not be meaningful if all cameras are concentrated in a very small area that will only capture a few individual animals, nor will it be representative of any larger area of interest if it focuses on a known concentration area. Jaguars are at the top of a trophic chain in habitats in which the biomass of terrestrial prey is often low. They must cover large areas to survive, and the lower the biomass of prey, the larger the home ranges. Numerous issues arise when a survey sample area is too small, including bias, which can lead to overestimates.

Surveys should include areas much greater than the home range of a single jaguar, as one cannot estimate population density by sampling at the scale of one animal. Radio-telemetry studies in Central America reported home ranges as small as 10-40 km² (Rabinowitz and Nottingham 1986) in Belize, but also larger, such as 32-59 km² (Ceballos et al. 2002) and 25-65 km² (Nuñez et al. 2002) in Mexico. Based on home range estimates generated in South America, it is reasonable to assume that some larger home range estimates will emerge from the next generation of telemetry studies in Central America. Home range estimates from South America have been larger, such as 51-108 km² in Venezuela (Scognamillo et al. 2003), and 34-263 km² in similar habitats in Brazil (Cavalcanti 2008, Cavalcanti and Gese 2009). The smaller ranges are females, the larger ranges are males. Unpublished estimates from colleagues in other study areas in South America have female ranges in excess of 300 km² and male ranges larger than that.

In simulations that varied home range estimates, numbers of camera trap stations, and sample area (camera trap station polygons), Tobler and Powell (2013) observed large positive bias (density overestimates) when camera trap polygons were small compared to home range estimates, but that simulations using sex covariates (separate male and female home range estimates) were unbiased when the camera trap survey polygon was equal to or larger than the size of one male's home range. They noted that in the Pantanal of Brazil, a polygon of 200-300km² (Cavalcanti and Gese 2009) might be sufficient. Their results still suggest that, in areas with low jaguar densities (<2 jaguars / 100 km²), the camera polygon might need to cover several home ranges in order to produce reliable density estimates.

Our recommendation of large sample areas focuses on males. Small female ranges guide the maximum spacing between stations. Noting the smallest home range size of jaguars in the Cockscomb Basin of Belize, Silver (2004) suggested 10 km^2 as a maximum gap area allowed between camera stations, with 3.6 km (the diameter of a circle with an area of 10 km^2) as the maximum straight line distance between cameras. This recommendation is safer when using the home range radius, but fortunately female home ranges in most areas are larger than 10km^2. Dillon and Kelly (2007) suggested that camera spacing should seek to maximize capture probability by including at least 2 stations per average home range, which aligns with Tobler and Powell's (2013) simulations that found the maximum spacing giving accurate results was about one-half the diameter of a home range.

Tobler and Powell (2013) found asymmetrical camera grid layouts reduced positive bias with density estimates *starting* to be unbiased when the longest side of the camera grid equaled one home range diameter. The analytical model used in these simulations (SECR in R) uses perfectly round home ranges. Since home ranges may be elliptical or irregular, this fascinating result merits testing with field data.

If an accurate density estimate is the goal, total samples must exceed estimated average male home range. If equipment and logistics force small sample areas, then the survey falls more into the spectrum of exploratory work, or an index based on number of individuals detected per effort (time and space), rather than a density estimate study.

Based on current telemetry-based knowledge on jaguar home ranges in Central American forests, Maffei et al. (2011*b)* recommend that the polygon formed by the camera traps should cover a minimum of 120 km^2 (Maffei et al. 2011*b*). The observation that a minimum of 45 camera stations are required to cover a polygon of 120 km^2 at 2 km spacing versus 20 stations at 3 km spacing demonstrates how spacing of units relates to equipment needs. Tobler and Powell (2013) suggest a minimum of 40-50 stations. When numbers of camera traps are limited, shifting the cameras across two or three sequentially deployed adjacent blocks of camera trap stations can help attain the size needed for a representative sample. In South America, where larger home ranges have been recorded, jaguar surveys should strive to cover 500-600 km^2 and, at the very minimum, camera trap station polygons should approach 300 km^2 (Maffei et al. 2011*a*, *b*). Tobler and Powell (2013) recommended polygons of 500-1000 km^2, which is scientifically valid, even if challenging logistically and financially.

There is no set minimum time for a mark and recapture study, as long as the sample provides adequate capture-recapture histories to generate a capture-probability-based estimate with scant bias and high precision; typically, low jaguar densities challenge those goals. Based on field experience, we have recommended minimal sample periods of 45-60 days for a single block survey, and nothing shorter than around 30 days when sequential blocks are employed. Because of their wide-ranging movements in search of productive areas of prey, even resident cats may cover considerable distances, with revisits to specific places potentially spaced at 7-10 day

intervals. Given that possibility, it has seemed sensible to allow enough time to capture those revisits in that general area, even if the total sample area may capture those cats elsewhere. Study duration is a tradeoff based on resources, but less so with current digital units than formerly with the first generation of film cameras, which required more frequent visits. Simulations run by Tobler and Powell (2013) resulted in reduced precision for a 30-day sampling period, and the authors recommended a minimum of 60 days when densities and encounter rates were high, or when sequential, adjacent blocks were used, suggesting data gained by longer sample periods (e.g., 90 days and more) justified the risk of violating the assumption of population closure.

If the number of cameras is limited, one approach for increasing the size of the trapping area is as follows (Silver 2004, Noss et al. 2013). Design two trapping patterns (i.e., grids) adjacent to each other and deploy them in two consecutive data collection periods. Using the full complement of cameras, collect data in the first grid for a "sub-sample" of the entire survey duration (e.g., 5 weeks), then move the cameras to the second grid for the same amount of time (in this case, 5 weeks for a total survey duration of 10 weeks). Typically, analyses have treated the resulting data set as if both grids were run simultaneously, even though they were not. All jaguars photographed on the first day of either grid are treated as photographed on Day 1; those photographed on Day 2 of either grid are treated as photographed on Day 2, etc. Animals photographed on different days are considered recaptures. This technique can be repeated again if necessary (i.e., additional grids incorporated), and the data analyzed the same way, but care should be taken to limit the total survey duration within the time required to satisfy the population closure assumption. The issues include: 1) recaptures of the same animal on day 2 on separate blocks (e.g., day 2, grid 1, day 2 grid 2); and 2) recaptures within blocks in a sampling sub-interval, both of which may result in lost data, because capture histories are registered by one record in each sub-interval. A method to describe capture histories developed to address these shortcomings is provided in Borchers and Efford (2008), Royle et al. (2009*b*), and tested in O'Brien and Kinnaird (2011).

When attempting to make inferences about a large area, it is rarely possible to sample the entire area of interest, and investigators should take care to select locations for sampling arrays that are representative of the area for which inferences are made. If the investigator wishes to make inferences beyond the effective sampling area (e.g., extend the inference from a sampling area to an entire park), then rules of stratification or random sampling should apply in determining the location of a sampling array. Often, sampling areas are chosen because they appear to be typical of the larger area of interest, or because they are easy to access. Representativeness, however, is not easy to assess subjectively, and easily accessible areas often are not typical of areas that are not easily accessed (O'Brien 2011).

Refining the Design

Once a basic design satisfies the assumptions, placement of the camera traps needs to be fine-tuned to optimize data collection. Camera placement is not necessarily random or strictly

systematic. Camera station locations should be selected to maximize the capture probabilities of individual target animals in the study area, while covering as large an area as possible to maximize the number of individuals photographed. This is a balance between positioning cameras closely enough to satisfy the assumption of all animals having a non-zero capture probability (as described above), and covering a large enough area to photograph more individual jaguars. It is also desirable for the animals in the study area to have similar capture probabilities, to the extent possible. While there are ways to account for variable probability of capture, estimations are simpler and more precise when capture probabilities are similar amongst animals. Because of this, a comparable density of camera traps throughout the sample area should be maintained. Placing many cameras within one animal's home range, while placing only a single camera within the range of another, should be avoided.

In a multi-species study to determine species abundance, O'Brien and Kinnaird (2011) divided a study area in Kenya into 2-km sample units, located the centroid within each, and deployed stations of two cameras spaced approximately 6-10 m apart at ecologically optimal sites within 50 m of the center point. This approach can work for jaguars. The tight spacing represents no risk and may ensure adequate data. However, to cover the large areas necessary to accommodate several jaguar home ranges in an efficient and sustainable manner, economy may suggest wider spacing. The specific placement of camera trap stations can maximize capture opportunities, and also may introduce unintended biased sampling. Deploying camera traps and following tracks in Venezuela in 1998, Polisar (personal observation) noted that males seemed to walk longer distances down open and semi-open dirt roads than females, which were more frequently photographed on smaller trails in forests. Many surveys across a variety of sites have used the jaguar's trait of seeking clear pathways to maximize capture probabilities (see Maffei et al. 2004 and Harmsen 2006), leading Maffei et al. (2011*b*), Tobler and Powell (2013), and Tobler et al. (2013) to recommend that abandoned roads and foot trails be used. Conde et al. (2010) found habitat differences between males and females in the Maya forest of southern Mexico, including road avoidance by females. The subtleties of differential road and trail use by genders, if extant and measurable, remain to be adequately quantified.

Many studies have recorded more males than females (Maffei et al. 2011*b*). While males are more mobile than females and thus more often photographed, there may be a risk of biasing all of the camera trap stations towards travel routes preferred by males. Conde et al. (2010) found significant habitat differences between genders, with males using relatively open areas with greater frequency, while females preferred thicker cover and avoided roads. These findings complement suggestions that gender-specific differences (in home range size) merit separate analysis models for males and females (Sollmann et al. 2011, Tobler and Powell 2013, Tobler et al. 2013). However, though Foster et al. (2010) suspected differences in habitats between genders, they found no significant differences. The recommendation to counter this ambiguity about open roads and narrow trails as a factor distinguishing male and female captures is an

attempt to strike a balance between good camera viewing fields with adequate cover nearby, and a diversity of micro-site types in the sample.

Setting Camera Traps

Once all of the above factors have been considered, the camera traps must be set. Below are suggestions from literature that guide the placement of camera traps.

- Find a spot where there are two suitable trees or posts on opposite sides of a trail. Suitable trees have trunks that are reasonably straight, thin enough to tie a chain or wire around, but not so thin that wind, people, or other animals can shake them excessively. Try to minimize direct sunlight on the cameras, as excessive heat can reduce the sensitivity of the sensors to endothermic animals. Cameras should be set back at least two meters from the nearest point where a target animal might travel across the sensor. This allows for clear, focused pictures and a large enough field of detection from the sensor. The longer the target animal is in the detection zone, the less chance of missing a photograph. Because the sensor beam should be approximately shoulder high, for a jaguar the camera should be set approximately 50-70 centimeters off the ground and parallel to it. Both cameras should be faced slightly down the trail to prevent mutual interference, but aimed at approximately the same point (Noss et al. 2013).

- Once the camera is set, clear the area between the camera and the path of travel of all vegetation that obstructs the beam or reduces the detection ability of the camera, which could result in obscured pictures. Large leaves and wavy grass can result in false triggers when the sun heats up a frond blowing in the wind. Also try to avoid pointing the cameras at objects in direct sunlight that may absorb heat and trigger sensors, such as large rocks or sunlit streams.

- Test the aim of both cameras by crossing in front of them. Do this on both the edges and the middle of the path. Most camera trap brands come equipped with an indicator light that will light up when the camera's sensor detects you. Approximate a target animal by walking in a crouch, and then walking in a more relaxed fashion. Make sure that every conceivable angle at which the target animal can pass in front of the camera is tested, and that in each instance a photograph is triggered.

- Occasionally, limitations in terrain or suitable trees hamper complete coverage of a trail. In that case, lay brush or other obstructions down one side of the trail to influence where the target species will walk. This technique is also useful if you are unable to set the camera well back from the trail, and wish to deter a target animal from passing so closely to a camera that it cannot take a well-focused picture. Appropriate fencing can also keep livestock away from cameras while permitting target animals to pass (Rosas-Rosas and Valdez 2006).

- Some studies have use scent attractants such as Calvin Klein's Obsession® or Chanel N° 5® (original or imitations) to lure jaguars in front of the camera traps. In the majority of cases the perfume has been sprayed on a piece of fabric or tampon attached to a stick, protected by a cut-off plastic bottle that prevents animals from removing the lure or rain from washing away the perfume, but allowing the scent to dissipate in the air. The stick is then fixed in the ground between the camera traps. The scent has to be replenished every week to 10 days. The lure probably does not draw animals from significant distances, but it can cause them to linger in front of the cameras, resulting in larger numbers of photos from various angles during each "capture" event, and thereby facilitating individual identification (Moreira Ramírez et al. 2011, Viscarra et al. 2011).

- Isasi-Catalá (2012) deployed cotton impregnated with a commercial imitation of Chanel No.5®, including tampons such as Tampax®, contained within a small baby food jar with the top sealed with tape but punctured with fine holes to allow the odor to escape gradually. In the center of the camera trap station a shrub or small tree was retained with the jar affixed at approximately 1 m above the ground, with the punctured top facing down to prevent water from entering. This prevented small animals from tampering with the jar, and a precise measurement of the height at which it was placed was useful as a reference for body size of visiting animals. Each time the station was visited, the cotton was impregnated with scent again. By all appearances, the scent caused the animals (a variety of species) to pause a moment in front of the camera traps, which facilitated identification, with the interpretation that this scent helped position the animals (out of their curiosity) in front of the lenses of the cameras.

The assumption in using scent to position animals is that, in a large study area, it is not attracting more target species into that area, rather it is positioning them (due to their curiousity) in front of the camera traps. Capture rates are not elevated by using scent, but the frequency of positive identifcations are (García-Anleu 2012).

Using Data for Indices of Species Not Identifiable to Individual Level

Systematic camera trapping surveys generate enormous datasets on non-target species, including prey species for jaguars. As they have done for jaguars, researchers have used such data opportunistically to describe abundance, activity patterns, and habitat use by these species. Researchers have also used datasets from systematic camera trap surveys to compare jaguars and other carnivores with prey species in terms of their abundance or density, activity patterns, or habitat use (Griffiths and van Schaik 1993, Laidlaw and Noordin 1998, O'Brien et al. 2003, Trolle and Kery 2003, Kawanishi and Sunquist 2004, Weckel et al. 2006, Johnson et al. 2006, Bowkett et al. 2007, Boas Goulart et al. 2009, Araguillín et al. 2010*b*, Montaño et al. 2010, Harmsen et al. 2010*b*, McCarthy et al. 2010, Espinosa-Andrade 2012). As with jaguar datasets, the data can be stored and analyzed using Excel, Access, or other database managers such as Mathias Tobler's Camera Base (for an application, see Tobler et al. 2008).

In most cases, researchers have used abundance indices, such as captures per 1,000 trap nights (considering records one hour or one day apart at the same camera station to be independent observations of the species), in order to compare prey species with jaguars, prey species among each other, or prey species across sites and years. In some cases researchers have used captures per 100 trap nights (Díaz-Pulido and Garrido 2012).

Capture frequency, expressed as captures per 1,000 trap nights (Gerber et al. 2010, O'Brien et al. 2010, Jenks et al. 2011), is calculated as number of photos of a given species multiplied by 1,000 and divided by the total trap nights during the survey (# of camera trap stations x length of the survey in days).

A survey designed specifically for jaguars will choose sites seeking to maximize captures of jaguars, such as roads and trails, not to maximize captures of the diverse array of prey species upon which jaguars depend, nor to ensure a random survey across the study area. Studies have therefore found significant differences in capture rates for prey species on roads versus trails (Trolle and Kéry 2005). Weckel et al. (2006) demonstrated that photo-capture rates of armadillos and pumas increased with distance from wider trails. Harmsen et al. (2010*b*) used 110 camera trap stations deployed across a variety of settings to evaluate effects of trails across species. They recorded higher capture rates for jaguars, pumas and ocelots on wider established trail systems. Brocket deer were negatively correlated with trail width. Paca and tapirs had higher capture rates on recently cut trails than established trails, and tapirs and possums increased with proximity to rivers and streams. Off-trail stations did not capture pumas, ocelots, or white lipped peccaries, had low capture rates of jaguars, armadillos, collared peccary and possums, but had high capture rates of red brocket deer, pacas and tapir (Harmsen et al. 2010*b*). Camera traps situated to maximize jaguar captures may miss particular micro-habitats or specific locations within the study area that particular prey species frequent (Harmsen et al. 2010*b*).

One risk to using camera-trap data as an index is that it may not distinguish few individuals photographed many times from many individuals photographed few times each. A single photo of a prey species that usually lives in groups, such as peccaries, includes many fewer visible individuals than are present. Complementary information from the study area is required, such as group size, to approximate densities and biomass.

Carbone et al. (2001) argued that photographic capture rates (photo captures per unit time) could be used as an index of density for species that cannot be individually identified. However, this requires describing and calibrating the relationship between capture rate and density, and measuring the precision of the calibration (Jennelle et al. 2002, Foster and Harmsen 2012).

In a study of tigers and their prey in Sumatra, O'Brien et al. (2003) classified all animals in photographs to species, recorded time and date, and rated each photo as a dependent or independent event, with independence based on: 1) consecutive photographs of different individuals of the same or different species; 2) consecutive photographs of individuals of the

same species taken more than 0.5 hours apart; or 3) nonconsecutive photos of individuals of the same species. The number of independent photographs was used as an index of species abundance. O'Brien et al. (2003) calculated two RAIs: RAI_1 measured days required to acquire a photograph; RAI_2 measured the number of photographs acquired per day, but was scaled up to photographs per 100 days (O'Brien et al. 2003). The relationships between RAI_1 and density estimates based on capture-recapture for tigers, and line-transect-based density estimates for other species (prey), were tested using linear regression and reduced major axis regression, which indicated that the number of photos provided a reliable index of density for tigers and their prey. Equivalent rigor was applied by Kinnaird and O'Brien (2012) in a study of large African mammals in rangeland in Kenya, testing the correlation of camera-trap-based RAIs against independent estimates of carnivore and ungulate abundance. The tight camera-trap spacing, cross-referencing of data types, and quality control in image catalogues in studies by O'Brien et al. (2003) and Kinnaird and O'Brien (2012) facilitate conclusions about a broad suite of species.

Camera-trap surveys may miss some potential prey species because of the habitats they occupy. Jaguars in some areas depend heavily on aquatic or semi-aquatic species, such as turtles and caimans, or semi-arboreal species that may be under-represented in camera trap surveys (Emmons 1987, 1989; Polisar et al. 2003; Weckel et al. 2006; Cavalcanti and Gese 2010; O'Brien et al. 2010).

Tobler et al. (2008) summarized some of the constraints in drawing conclusions from comparisons of capture frequencies across species:

We believe that capture frequencies are a relatively poor index for relative abundance among surveys or for comparing relative abundance of species within surveys because of a variety of factors such as species-specific behavior [e.g. use or avoidance of trails…, partly arboreal versus exclusively terrestrial, or habitat specialist versus generalist], species size (large animals are more likely to trigger the cameras), home range size (animals with larger home ranges move around more and have more cameras within their home ranges) or simply stochastic variation as can be seen when looking at the large differences in capture frequencies for several species.

Foster and Harmsen (2012) cautioned against using surveys designed for one species for other species that may use habitats quite differently:

Using the same survey design for multiple species may produce imprecise density estimates because the optimal trap location, spacing, and minimum survey area for one species may not be optimal for another species…. Inter-specific variation in capture rate may reflect a difference in abundance or detection probability between the species (or a combination of both).

For broader faunal inventories, the relatively tightly spaced semi-systematic placement of camera-trap stations practiced by O'Brien and Kinnaird (2011) and Kinnaird and O'Brien (2012) may be a solution. According to Caughley (1977) quoted in (Williams et al. 2002): *An index of*

abundance or density is any correlative of density. The key word is the *correlation* between capture frequency and actual abundance. Usually there is a positive relationship between capture frequencies and abundance or density. At the same time, rarely has it been established that an index measures a constant proportion of the population. As a result, varying detection probabilities could cause mistaken assumptions of contrasts in abundance (Conn et al. 2004).

Indices generated by camera trap surveys will have their greatest utility when comparing within-species within-site frequencies obtained by sampling that has kept camera trap stations, habitats, and sampling space and time constant, and even then exercising caution. With no measure of confidence, and considerable sampling noise, even within-species contrasts must indeed be strong to be considered valid reflections of real contrasts or trends in the system being sampled (Conn et al. 2004). In the absence of a measure of detection probability, or proven monotonic relationships with independent estimates, subtle contrasts may result from sampling and/or natural variation other than abundance.

Some surveys have placed cameras at salt licks (Araguillín et al. 2010*a*) and waterholes. All of these can record prey species, but with potential bias that: 1) must be recognized; and 2) is difficult to measure. For example, if salt licks tend to attract more ungulates than other prey species, then abundance of these species may be overestimated. Using the data to draw conclusions might overestimate ungulate abundance.

Occupancy Surveys

An alternative method for estimating relative abundance spatially, rather than strictly numerically, is "patch occupancy" (MacKenzie et al. 2002, 2003; MacKenzie and Royle 2005; McShea et al. 2009; Licona et al. 2011; O'Connell and Bailey 2011). Camera-trap data can also be analyzed using occupancy models to evaluate habitat use within survey areas, relative abundance across wide areas, or species diversity based on observed species and the number of additional species present but not observed (MacKenzie et al. 2006; O'Brien 2008; Tobler et al. 2008*a*, *b*). A "naive" spatial index is simply the proportion of camera stations where the target species appears, and even if drawing no additional conclusions about the target species, interesting presence-absence inferences about the distribution of prey species can be obtained. The occupancy modeling software PRESENCE 5.5 (Hines 2012, http://www.mbr-pwrc.usgs.gov/software/presence.html) statistically estimates the proportion of camera stations where the target species is present, according to capture probabilities, even though the species may not be recorded in as many camera stations. Just as CAPTURE uses capture-recapture histories to estimate the total number of individuals present, including un-observed individuals, PRESENCE uses capture-recapture histories in detection-based probability models to estimate the total number of camera trap stations where the species is present, including camera stations where the species was not observed.

If data are sufficient, complex patch occupancy analyses can incorporate additional variables in order to evaluate habitat preferences or responses to anthropogenic pressures. Sollmann et al. (2012) used camera-trap-based occupancy modeling to examine jaguar and puma correlations with water, roads, and dense habitats. Karanth et al. (2011) examined the influence of prey abundance and human disturbance in field-sign-based tiger occupancy surveys. The covariates Zeller et al. (2011) examined when analyzing interview based occupancy surveys for jaguar prey included proportions of forest, wetland, water, and distance to edge of protected area.

Understanding the dynamic distribution of a species within a conservation area is a critical metric in adaptive management. Occupancy analyses can estimate the proportion of an area that a species occupies, and is a method that can be repeated to evaluate expansions and retractions of range. By incorporating potential explanatory variables, the effect of habitat characteristics and anthropogenic factors, as well as the effects of management interventions, can be explored. The field data used to estimate occupancy can come from a variety of sources, including camera traps (Kinnaird and O'Brien 2012).

Additional Details on Survey Design and Analyses

Males vs. females: Camera traps frequently permit confirmation of the sex of photographed animals. However, researchers often do not know what the actual sex ratios of target species are in the study site. Therefore, they are unable to confirm biases in sex ratios of individuals identified from camera traps; for example, if frequent male bias in jaguar surveys (Silver et al. 2004, Maffei et al. 2011*a*) reflects a real male bias in the landscape. The observed bias may result from methodological issues combined with behavioral differences between the sexes, resulting in lower capture probability for females at the camera trap locations established for the survey. Assuming that females are less detectable than males and move smaller distances (as confirmed for tigers; Karanth et al. 2011), one solution is to estimate density separately for males and females, respectively, rather than pooling all individuals together in a single analysis (Sollmann et al. 2011, Tobler et al. 2013).

Niche partioning: Camera trap records of activity are also used to evaluate niche partitioning among sympatric species (di Bitetti et al. 2009, Harmsen et al. 2009, Monroy-Vilchis et al. 2009, Ridout and Linkie 2009, Romero-Muñoz et al. 2010), temporal and spatial relationships between predators and prey, or relationships between wildlife activity and human interventions (Griffiths and van Schaik 1993, Laidlaw and Noordin 1998, Kawanishi and Sunquist 2004, Johnson et al. 2006, Weckel et al. 2006, Ngoprasert et al. 2007, Lucherini et al. 2009, Paviolo et al. 2009, Davis et al. 2011, Harmsen et al. 2011). Aside from time of day, some digital cameras are capable of recording environmental data for each photo, such as temperature and relative humidity, which are factors that may be of interest in particular studies.

Habitat use: A number of studies postulate habitat preferences for a variety of species by comparing camera trap abundance indices across categories of habitats in which camera traps are

placed (Trolle 2003, Bowkett et al. 2007, Boas Goulart et al. 2009, Foster et al. 2010*a*, Harmsen et al. 2010*b*, Davis et al. 2011).

Survival/population turnover: In cases where individuals are identifiable over extended time periods (multiple seasons/years) and camera trap surveys can be repeated, open population analyses are possible (O'Brien 2011). Karanth et al. (2006, 2011*b*) used camera trap data on tigers in conjunction with open population capture-recapture models to estimate key demographic parameters, such as time-specific abundance, annual survival rate, and number of new recruits. Balme et al. (2009*b*) used camera trap surveys before and after conservation interventions to reduce human-leopard conflicts, finding that annual leopard population growth rate increased significantly. Gardner et al. (2010) and Royle and Gardner (2011) provide details of how to formulate and run a series of hierarchical spatial capture-recapture models, and to extend them to demographically open populations, using WinBUGS.

Complementary methods for density estimates: Whenever possible, density estimates derived from camera trap surveys should be compared with other available information on the species at the site or at similar sites. For example, researchers have conducted camera trap surveys simultaneously with radio-telemetry in the case of jaguars (Soisalo and Cavalcanti 2006) and ocelots (Maffei and Noss 2008), and with scat DNA in the case of tigers (Gopalaswamy et al. 2012*a*) and snow leopards (Janečka et al. 2011). Scat DNA data can be analyzed using the same SECR methods described above in order to estimate density. Radio telemetry provides invaluable information for designing appropriate camera trap surveys on ranging behavior and habitat use (Rabinowitz and Nottingham 1986, Nuñez et al. 2002, Scognamillo et al. 2003, Cullen Jr et al. 2005, Cavalcanti 2008, Cavalcanti and Gese 2009, Conde et al. 2010). Sampling designs that include overlapping methods to compare the results allow calibrations and validations, and evaluate the strengths and weaknesses of each method.

Density Estimation

The following section discusses design and analysis considerations when camera traps are used with a jaguar density estimate as the goal. The program CAPTURE generates an estimate of abundance, not of density, which researchers have derived by calculating a survey area equivalent to a polygon sampled by the camera traps, buffered by ½ or the full MMDM by individuals of the target species during the survey (Wilson and Anderson 1985, Karanth and Nichols 2002, O'Brien 2011). This "effective sample area" (as opposed to the camera trap polygon, which is defined by the outer limits of the stations) has been necessary to take into account those individuals whose home range was only partly in the polygon, and to avoid estimating a population density based on a "cross-roads effect," where jaguar ranges happen to overlap. The buffer is drawn as a circle around all stations, as well as the outer limit of these stations, and also as a set distance around the camera trap station polygon, as well as the outer limit of this polygon (Silver 2004). This approach has no theoretical mechanism to link abundance with the survey area in order to estimate density (Williams et al. 2002, Royle et al.

2009*b*), and has been questioned due to the *ad hoc* nature of estimating the survey area (Efford 2004, Gardner et al. 2009, Royle et al. 2009*b*, Gopalaswamy et al. 2011) and because it depends directly on the size of the survey area (Maffei et al. 2011*a*, *b*; Tobler and Powell 2013).

The most severe issues with this approach have been related to small sample areas defining the limits of measurable movement, thus underestimating the potential ranges of the cats and resulting in overestimated densities. Soisalo and Cavalcanti (2006) tested telemetry-based density estimates against CAPTURE-based density estimates, finding better agreement with full MMDM. Recommendations from Maffei and Noss (2008), Maffei et al. (2011*a*), and Maffei et al. (2011*b*) agreed with Soisalo and Cavalcanti (2006)'s conclusions that the full MMDM was less prone to bias results than ½ MMDM, and then only when combined with large sample areas that were based on estimations of local home range sizes.

Maffei et al. (2011*a*) recommended that many of the first generation of density estimates be treated as preliminary until more large sample areas had been tested (e.g., >500km²), and that future research should emphasize larger survey areas to confirm whether density estimates are consistent when the scale of the survey is increased. Foster and Harmsen (2012) discussed the issue of effective trapping area (ETA) in detail, clearly stating the circular logic of defining home range/movement lengths by size of area sampled and urging more examination (including simulations) of the conditions under which the above described MMDM methods might perform satisfactorily. Because male and female jaguar ranges differ greatly in size, Foster and Harmsen (2012) also suggested that gender specific estimates of MMDM might reduce heterogeneity in the data, suggesting separate density estimates.

Sollmann et al. (2011) and Tobler and Powell (2013) subsequently explored gender specific analyses in relation to density estimation, noting positive results, although dividing already small samples by gender pushed the limits of the SECR models they were using. Meanwhile, preliminary results based on published (Noss et al. 2012) and unpublished data (Garcia-Anleu, Perera, Diaz Santos) analyzed from several additional sites with the two SECR models suggest that when using large polygons, density estimates generated by CAPTURE are in rough agreement. Using simulated data, Tobler and Powell (2013) suggested full MMDM, with their results indicating unbiased results for camera polygon sizes equal to or larger than one male home range.

The frustrations with the *ad hoc* areal estimates CAPTURE requires contributed to the development of SECR models. This approach directly estimates animal density by using information on capture histories in combination with the location of the individual capture under either a Bayesian or likelihood analysis framework (Borchers and Efford 2008, Royle and Young 2008, Gardner et al. 2009, Royle et al. 2009*b*, Royle and Gardner 2011).

Key assumptions of the SECR models are that animals occupy home ranges, home ranges are circular and are dispersed randomly, and successive trapping occasions are independent. The

probability of capture is a declining function of distance between the range centers and camera traps, directly analogous to a detection function in distance sampling (Efford 2004, Royle et al. 2009*b*).

Efford et al. (2004, 2009) and Efford and Fewster (2013) offer the software package DENSITY (http://www.otago.ac.nz/density), which operates in a Windows interface and requires two input files: trap layout (numbered location) and capture data (i.e., numerical designations for sampling session, animal identification, trap day, and trap location). Additional information required includes trap layout type and a buffer value recommended to be several times the estimated home range diameter for the target species, which establishes for the analysis a state space area that encompasses the survey area, but extends well beyond it on all sides.

Currently, two packages for running SECR models in the programming language R (see Box 2) are available: an R version of DENSITY called SECR, and SPACECAP.

The R package SECR, developed by Efford et al. (2009) and Efford and Fewster (2013), utilizes the likelihood approach to SECR models, and working details and instructions are provided in http://www.otago.ac.nz/density/SECRinR.html.

The R package SPACECAP applies the Bayesian approach, specifying the same model as is carried out in the R package SECR, but using Markov-chain Monte Carlo (MCMC) to simulate draws of each home range center from the posterior distribution (Gardner et al. 2009, Royle et al. 2009*a*, *b*, Reppucci et al. 2011, Gopalaswamy et al. 2012*b*). The software package is available at http://cran.r-project.org/, and Gopalaswamy et al. (2011) provide a detailed manual.

While the SECR models are new, they offer promising results. The assumptions they make about home ranges are not entirely realistic, but are an improvement over estimation bias obtained with CAPTURE analyses generated from survey areas that are too small. Initial analyses suggest that when sample areas are large enough (several hundred square kilometers), which removes over-estimate bias with ad hoc sample area estimates for CAPTURE, the results generated using CAPTURE, DENSITY, and SPACECAP are all in rough agreement. Tobler et al. (2013) suggest an interesting option of using home-range parameters derived from large sample areas to improve estimates made from previous sample areas that were too small.

Hair Collection

Many researchers are focusing on hair-snare sampling techniques as a non-invasive alternative to estimate number and density of large carnivores (e.g., Kendall and McKelvey 2008; Kendall et al. 2008, 2009). With these techniques, individuals are attracted to sampling stations with a scent lure (although in some instances baits are used). Sampling is usually done in grid cells (established at a scale determined by species biology, question(s) of interest, and logistical considerations) using hair-snare “corrals” that are built by running a single strand of barbed wire at a pre-determined, optimal height for the species of interest around several trees, posts, or

similar structures (e.g., Woods et al. 1999, Atwood et al. 2011). When the individual passes under the wire, a small tuft of hair is snagged. The follicles from the hair samples contain DNA, which can be used to identify individual animals. Alternatively, barbed wire or other means of passive hair collection can be attached to a natural rub tree or another tree/post associated with a lure, and for some species (such as bears) natural rub trees can detect individuals not sampled by barbed wire "corrals" (e.g., Boulanger et al. 2008, Stetz et al. 2010, Kelly et al. 2012). Placement of hair-snag locations within a grid is usually determined based on sign, natural travel routes, habitat type, and/or prey availability, and should be maintained a minimum distance (determined by sampling design and species biology) between hair-snags located in adjacent cells. Once capture "corrals" are baited, these are usually run for multiple capture sessions generally consisting of 7-21 day periods, although length of capture session can vary (e.g., Atwood et al. 2011). The use of a single lure and a standard volume should control for lure-induced variation in habitat-specific detection probabilities (MacKenzie et al. 2006). To prevent contamination, forceps are used to collect hair samples from barbs, and individual samples are generally stored in small-sized envelopes. Once hair samples are collected, all barbs in a corral or rub location should be flamed to prevent cross-contamination prior to the next sampling period.

For felids, McDaniel et al. (2000) developed a protocol for using a baited hair-collecting pad based on roofing nails for Canada lynx (*Lynx canadensis*), and, as Kelly et al. (2012) point out, this technique has been successfully used to sample Eurasian lynxes (*Lynx lynx*; Schmidt and Kowalczyk 2006) and ocelots (Weaver et al. 2005), among other species. Generally for felids, the use of hair-snare sampling designs has had mixed success. Although successful for lynx (e.g., Mills et al. 2000), in many studies detection rates have been fairly low for bobcats (Lynx rufus; e.g., Harrison 2006, Long et al. 2007*a*) and pumas (e.g., Sawaya and Ruth 2006). Similarly, as reported by García-Alaníz et al. (2010), to our knowledge the collection of jaguar hair samples using hair-snare sampling techniques in the wild has not been reported to-date (see discussion below). For a comprehensive discussion on hair collection, including techniques for felids, see Kendall and McKelvey (2008).

Utility, Considerations, and Limitations of Hair Snare Techniques for Jaguars

As mentioned previously, García-Alaníz et al. (2010) reported that the collection of jaguar hair using hair-snare sampling techniques in the wild has not been successful. Similarly, for other large cats such as mountain lions, data have been sparse, with low returns based on hair-snare sampling designs (Shinn 2002, Ruell and Crooks 2006, Downey et al. 2007, García-Alaníz et al. 2010). The use of hair-snare techniques to sample for large felids has often resulted in more samples from non-target mammalian species. García-Alaníz et al. (2010) postulate that this might be due to the nature of felid hair, which are very short and fine compared to the coarser hair found in many canids (dogs), ursids (bears), and mustelids (e.g., weasels) (Woods et al. 1999, Mowat and Strobeck 2000, Mowat and Paetkau 2002, Kendall and McKelvey 2008). Similarly, Portella et al. (2013) had very limited success with various lures and hair snares for neotropical felids, including jaguars in wild settings.

In addition to limited success of these techniques for many species of felids, another concern is the relatively low amount of DNA found in hair follicles. According to Kelly et al. (2012), multiple hairs can be pooled to increase DNA yield for species' detection studies; however, pooling multiple hairs is risky because it can create false genotypic individuals (see Gagneux et al. 1997, Alpers et al. 2003, Roon et al. 2005*a*, *b*). Kelly et al. (2012) suggest that researchers either accept the low DNA yield from single hairs, or consider developing a hair-snag sampling protocol/system that allows only one animal to rub it (Beier et al. 2005, Bremner-Harrison et al. 2006).

Finally, these techniques are labor-intensive (e.g., Kendall et al. 2008), relatively expensive (Kendall and McKelvey 2008), and typically have problems identifying the area inhabited by the estimated population, although occupancy modeling efforts can alleviate much of this concern (see MacKenzie et al. 2006, Kendall and McKelvey 2008). For these reasons, these techniques should be used for felids with caution and a complete understanding of their limitations. Further, hair-collection techniques should only be considered when used with other tools for detecting neotropical felids such as jaguars.

Fecal DNA and Scat Detection Dogs

Recent advances in molecular genetics make fecal DNA technology a promising and viable option for researchers working on species that are difficult to capture and mark (due to biological and political factors), detect species presence-absence, identify sex of each individual, and determine identity of each individual. Fecal analyses have been used in the past to examine food habits, relative abundance of animals, disease, infer habitat use, and estimate home range size (Smith et al. 2003, Waits and Paetkau 2005, Beja-Pereira et al. 2009). DNA technology has advanced such that a well-designed study can use fecal DNA sampling to determine species, sex ratio, home range, and even produce population estimates for carnivores through these non-invasive approaches (Kohn et al. 1999; Smith et al. 2003; Boulanger et al. 2004; McKelvey and Schwartz 2004*a*, *b*; Paetkau 2004; Marucco et al. 2009; Brøseth et al. 2010; Stenglein et al. 2011). Acquiring data from scats of rare carnivores requires sampling and surveying across large areas of the landscape.

The use of detection dogs to obtain DNA from scat of carnivores and other species has begun to be used intensively in the last several years (Smith et al. 2003, Wasser et al. 2004, Long et al. 2007*b*, MacKay et al. 2008, Vynne et al. 2011). Using detection dogs specifically trained to locate the scat of target species, in this case jaguars, seems to be a promising non-invasive approach to sampling rare carnivores on the landscape. Dogs have already been used to locate scat of species that range from commonly-occurring on the landscape to threatened and endangered species, including some listed under the United States Endangered Species Act. These include, but are not limited to, jaguars (Wultsch 2008, Vynne et al. 2011, Wultsch et al. 2011), black bears (*Ursus americanus*) and grizzly bears (Wasser et al. 2004, Beckmann et al. 2013), San Joaquin kit foxes (*Vulpes macrotis mutica*; Smith et al. 2001, 2003, 2005, 2006),

black-footed ferrets (*Mustela nigripes*; Dean 1979, Winter 1981, Reindl-Thompson et al. 2006), bobcat (Harrison 2006, Long et al. 2007*b*), fisher (Martes pennanti; Long et al. 2007*b*) and right whale (*Eubalaena glacialis*; Rolland et al. 2006), among others. In fact, in one study dogs have been used to detect the presence-absence of a target species, kit fox, with 100% accuracy despite the presence of sympatric striped skunks (*Mephitis mephitis*) and American badgers (*Taxidea taxus*) (Smith et al. 2001, 2003). This sampling technique has merit as a useful tool for ecologists addressing landscape-scale conservation issues, such as habitat selection/suitability and connectivity for populations of rare, large carnivores (MacKay et al. 2008). Detection dogs are a useful technique to sample complex matrices of public and private lands for carnivores by reducing the difficulty in acquiring animal-handling permits and by reducing some costs (e.g., up-front costs associated with GPS collars). In some instances, particularly for rare and wide-ranging species such as jaguars in the southwestern United States, trained detection dogs can sample carnivores more effectively than traditional methods, such as hair snares, scent stations, and camera traps (Wasser et al. 2004, Harrison 2006, Long et al. 2007*a*).

Sampling with Dogs

Detection dogs (breed generally does not matter as much as ball drive [motivation to play with a ball as a reward for a task that is performed] and trainability) can be trained to detect scat of target species using the techniques described in Smith et al. (2003). One significant advantage is that detection dogs can be trained to locate the scat of multiple target species simultaneously, thus potentially saving costs and effort (e.g., Beckmann 2006, Vynne et al. 2011). Generally dogs are trained with scats of wild origin from each of the focal species, but training scats can also be supplemented with scats from captive animals fed a similar diet to wild individuals. As a dog's work experience can range from none (not yet fielded for detection of naturally-occurring scats) to many seasons in the field detecting scats, specific training can range from 2 to 5 weeks. During training, dogs generally progress from scent recognition in scent line-ups to handler-blind off-leash simultaneous searching for—and locating—all focal scats.

Sampling using detection dogs can follow line transect methods or some form of a block design depending on question(s), study area, species, and desired data coupled with planned analyses. In a block design, the study area is gridded off in some predetermined grid-cell size, with each block/grid containing a sampling transect along which the dogs sample. The survey unit size (i.e., block and/or transect length) is generally determined based on mean home-range size or similar parameter of the target species using data reported in the literature in the same system (or similar systems) so as to be able to detect the species of interest.

DNA analyses

A portion of each scat located by detection dogs can be collected in 95% ethanol in the field for preservation and transport (see Frantzen et al. 1998 for discussion on fecal preservation methods). DNA can be extracted using a QIAGEN stool kit following manufacturer's protocol

(Qiagen, Valencia, California, USA). Extractions should be carried out in a room dedicated to low quantity DNA sources to minimize contamination risk. Negative controls (no scat added) should also be included in all DNA extractions and PCRs to test for contamination. Species identification can be performed via a 2-step process described in detail in Onorato et al. (2006). The first screening generally includes amplification of a short section of the mitochondrial DNA (mtDNA) control region using species identification SpID primers. Samples that fail to amplify using the SpID primers should be subsequently amplified a second time. If a sample fails both times, sequencing can then be attempted with mtDNA cytochrome B primers (Farrell et al. 2000) using protocols described in Onorato et al. (2006). Species identification of sequenced scats can be conducted by comparing results with known sequences for the target species and with entries in GenBank using the BLAST program (National Center for Biotechnology Information).

Utility, considerations, and limitations of detection dogs

The use of detection dogs coupled with genetic analyses and habitat models (e.g., resource selection function), occupancy modeling, and/or connectivity models (e.g., Circuitscape®) is promising, providing useful techniques to model and monitor recovery efforts of large carnivores and other species as they continue to expand their current range and populations in the coming decades (e.g., Vynne et al. 2011, Wasser et al. 2012). However, as with any sampling technique, there exist several limitations and other data collection considerations (see Beckmann 2006 for a detailed discussion). In the past, one large drawback of this sampling technique was that the dogs often outworked the DNA lab, finding scat samples that were too old and degraded to be suitable for DNA amplification (although this has generally been limited to producing individual DNA fingerprints as opposed to species identification; Beckmann 2006). As DNA labs have advanced in the ability to obtain DNA from low-quality sources (such as scat), this problem has lessened in recent years. Although DNA can often be obtained that allow for species identification, in some cases it is still challenging to produce individual DNA fingerprints from scat data. Thus, certain questions, such as population size estimates, may be difficult to assess through a mark-recapture design using detection dogs.

Additionally, to-date little work has been done to assess and quantify differences in detection rates between different dogs (both across breeds and between individual detection dogs) and between different habitats or conditions as environmental variables change, although there are exceptions (e.g., Hatch 1997, Vynne et al. 2011). Wind speed, relative humidity, topography, age of sample, and temperature all influence the scent cones left by scat samples (Wasser et al. 2004), yet few models currently exist for predicting the shape and size that scent cones (as scent leaves a source it takes the form of a cone, being narrower at the source and wider further from the source) take under various environmental conditions. Thus, accurately predicting the likelihood of detection by dogs under various conditions is currently a large question that needs to be resolved, especially if a goal is to use data collected by detection dogs in occupancy modeling efforts or other methods where detection probability is of concern (see Vynne et al.

2011). Other methodological questions surrounding detection dogs as a technique and an overview of costs/benefits are reviewed in Beckmann (2006).

Telemetry

Radio-telemetry (including very-high frequency [VHF] and global positioning systems [GPS]) provides the opportunity to monitor and map detailed movements of the most highly mobile and cryptic animals. These data provide tremendous opportunities to answer behavioral and ecological questions and to promote quantitative and mechanistic analyses (Millspaugh and Marzluff 2001, Cagnacci et al. 2010, Miller et al. 2010). Specific to surveying and monitoring of jaguars and other large felids, these tracking technologies have often been used to monitor ecological and population parameters.

Methods used to capture and handle jaguars to deploy telemetry devices are presented in Appendix 1.

Ecological Monitoring

Wildlife tracking technologies have been used to estimate jaguar home-range size, daily and dispersal movement distances, and habitat associations. Jaguars have relatively large home ranges which are highly variable and vary with topography, prey availability, and population dynamics (Brown and López-González 2001). Published mean home range size for male jaguars in tropical America, from which data are most abundant, vary from 12.8 to 165.8 km^2 (U.S. Fish and Widlife Service 2012). Only one limited jaguar home-range study has been conducted in northwestern Mexico, specifically in the municipality of Sahuaripa, Sonora. One adult female jaguar occupied an area of 100 km^2 for four months during the dry season (López-González 2011 as cited in U.S. Fish and Wildlife Service 2012). Núñez-Pérez (2006) reported average male and female jaguar home ranges of 100.3 ± 15.0 km^2 and 42.5 ± 16.0 km^2, respectively in a study of sympatric jaguars and pumas in the Chamela-Cuixmala Biosphere Reserve in Jalisco. No VHF or GPS-based home range estimates exist for jaguars in the southwestern United States.

Like most large carnivores, jaguars are capable of long-distance daily and dispersal movements. VHF and GPS technologies offer an effective means of tracking long-distance movements. Jaguars have been documented to move up to 20 km in one night in coastal Jalisco (Nuñez et al. 2002) and disperse up to 70 km in coastal Jalisco and Brazil (Nuñez et al. 2002, Rabinowitz and Zeller 2010).

VHF and GPS technologies have offered insights into the wide-range of vegetation and habitat elements selected by jaguars. Crawshaw and Quigley (1991) found six (2M:4F) radio-marked jaguars used gallery forest and forest patches more than expected and open forest and grassland less than expected in the Pantanal region of southwestern Brazil. Similarly, Cavalcanti (2008) found ten (6M:4F) GPS-marked jaguars selected forests and shrublands and avoided more open habitat types. Cavalcanti (2008) also located jaguars closer to permanent sources of water than

expected. In the Venezuelan llanos, Scognamillo et al. (2003) found jaguars using habitats (flooding savannas, dry forest, dry savanna with chaparro, semi-deciduous forest, dry pasture, evergreen forest) in the same proportion as available within their home range. In the Upper Paraná River region of Brazil, Cullen Jr et al. (2013) found ten radio-marked jaguars selected dense marshes and primary forests and avoided human-dominated areas, such as open pastures.

Population Monitoring

Density

Estimation of animal density is fundamental to ecology. Ivan et al. (2013) stated:

> *Density is used to evaluate system responses to environmental perturbations and treatments* (Converse et al. 2006, Manning and Edge 2008), *it can function as a benchmark for listed species recovery (U.S. Fish and Wildlife Service 1998:319), it can be useful for understanding system dynamics* (Soulé et al. 2003), *or assessing habitat suitability for dependent species* (Zahratka and Shenk 2008), *and it is routinely used in population monitoring and modeling* (Thompson et al. 1998).

Estimates of population size are most often developed using a grid of detection devices (e.g., traps, cameras, hair snares) to build detection histories of individual animals (refer to the capture-recapture model section above for statistical and other details). Estimates of abundance are then calculated using closed-capture models (Otis 1978, White et al. 1982, Williams et al. 2002). These models assume both demographic (i.e., no births, deaths, immigration, or emigration) and geographic closure (i.e., no movement on or off the study site) of the study population during the sampling period. Short sampling periods informed by the natural history of the species of interest often satisfy the assumption of demographic closure. However, in most cases, geographic closure is unlikely (White et al. 1982). These estimates of abundance are thus difficult to convert to density because the area effectively sampled by the detection devices is unknown.

The most common strategy to account for geographic closure is to estimate the effective area sampled. The abundance estimate obtained from closed-capture models is then divided by the estimate of the effective area to obtain an estimate of density. Detections are used to estimate the MMDM by each individual during the sampling session. The effective area sampled is then defined as the study site buffered by this distance or one-half this distance (Wilson and Anderson 1985). This strategy has been used to develop estimates of jaguar density across the distribution (see reviews in Maffei et al. 2011*a*, *b*; Foster and Harmsen 2012; Noss et al. 2012; Tobler and Powell 2013).

Alternatively, estimates of effective area sampled have been developed using telemetry locations to calculate the buffer width to apply to the study site (Soisalo and Cavalcanti 2006; Maffei and Noss 2008; Maffei et al. 2011*a*, *b*; Núñez-Pérez 2011; Tobler and Powell 2013). These studies

have calibrated MMDM-based estimates with estimates of "actual MMDM" based on telemetry movement data concluding that estimates using the full MMDM were less prone to over-estimation bias than ½ MMDM-based estimates (Noss et al. 2013). Even then, in most cases MMDM estimates developed using detections have been constrained by the distances between detection devices, hence researchers (Maffei et al. 2002, 2011*a*, Noss et al. 2013, Tobler and Powell 2013) have been urging larger sample areas less prone to this constraint.

Most recently, Ivan et al. (2013) present a density estimator which uses an alternative application of telemetry data to address geographic closure. The approach is rooted in the idea of estimating fractions of animals or "animal equivalents" within an area. It is reported to overcome the potential biases of MMDM and SECR models if animal movement and detection are unnaturally affected by the sampling process. Ivan et al. (2013) state: "The method allows home range shifts or irregular movements induced by sampling, makes no assumptions about the distribution and movements of animals on the landscape, and does not require estimation of effective area sampled." We are unaware of any applications of this method yet to the estimation of density for jaguars or other large felids.

Survival

Radio-telemetry provides an opportunity to determine the rates at which animals die, relate covariates to rates of survival (e.g., age-class, sex, resource availability), and identify sources of mortality. In survival studies, radio-marked animals are followed closely to determine whether they live or die between sampling periods, detecting each individual during each sampling period in which it is alive.

The two most common analytical frameworks, Kaplan-Meier and Cox proportional hazard models, have been used to estimate survival rates and assess the influence of covariates on survival for select populations of large felids.

The staggered entry Kaplan-Meier method (referred to as the "known fates" option in program MARK) is widely used to estimate survival of a radio-marked populations and investigate the influence of covariates on survival probabilities (Pollock et al. 1989*a*, *b*). This method allows animals to be added to the study while it is in progress and to be censored if animals leave the study area or lose their radio tags. The standard model assumes that censoring is independent of animal fate; that is, disappearance of an animal is not associated with death. Banerjee and Jhala (2012) used the Kaplan-Meier method to calculate life stage-specific annual survival rates for 20 Asiatic lions (*Panthera leo persica*) in India that were monitored using radio-telemetry between 2000 and 2010.

The Cox proportional hazard model (Cox 1972, Venables and Ripley 1994) is a regression-based alternative to calculating survival rates and relating survival to covariates. This method is often preferred over Kaplan-Meier when: 1) there are several explanatory variables, particularly when some of these are continuous, 2) fates of individuals are not known for various reasons, 3) the

study is stopped before collars are lost, and 4) all individuals have died. Riggs and Pollock (1992) provide a detailed application of the model. Goodrich et al. (2008) used Cox proportional hazard models to find that survival rates varied among sex-age classes of 42 Amur tigers (*Panthera tigris altaica*) in Russia that were monitored using radio-telemetry between 1992 and 2005.

Studies investigating survival via telemetry are also often able to determine and quantify sources of mortality. This information is often critical in developing effective conservation strategies. For example, Goodrich et al. (2008) found poaching to be the largest source of mortality for Amur tigers, particularly for dispersing individuals. For jaguars, studies investigating sources of mortality via telemetry have not been conducted; instead, studies have been limited to interview-based surveys of local inhabitants (e.g., Foster 2008, Carvalho and Pezzuti 2010).

VHF and GPS tracking technologies provide a wide array of opportunities to examine detailed ecological and conservation questions related to jaguar movement, home range, habitat use, survival, productivity, population estimation, and behavior (Miller et al. 2010). These technologies provide the ability to remotely monitor elusive, wide-ranging jaguars while they pursue their normal movements and activities. We acknowledge these technologies are not the appropriate tools to answer all ecological and conservation questions. However, these technologies provide opportunities to make great advances in our understanding of jaguar ecology and apply this knowledge to current efforts to conserve jaguars and jaguar habitat.

Population Genetics

Genetic analysis can reveal population connectivity on massive scales that extend back in time, and across continents. They can also let us see and understand current population relationships in ways that no other tools can. Below we present some examples of what these powerful tools can tell us, on an ancient range wide scale, and on a more recent biome wide level.

When Eizirik et al. (2001) investigated the genetic diversity, population structure, and demographic history of jaguars across most of their geographical range with a sample from ~ 40 individuals from Mexico to southern Brazil, their analyses found an absence of deep geographical subdivision, evidence for recent and incomplete isolation among major regions, and the inference of historically high levels of gene flow. There was evidence of up to four incompletely isolated phylogeographic partitions between southern and northern South America (below and above the Amazon River), southern Central America, and Guatemala into Mexico. The Amazon River appeared to have been less an impediment for male dispersal than females, which follows the tendency in felids in which females are largely philopatric (tending to return to or remain near a particular site or area) and males are more likely to disperse longer distances (Eizirik et al. 2001). Ruiz-Garcia et al. (2006) examined heterogeneity and gene flow of jaguars in Colombia to test the strength of two proposed subspecies. Despite evidence suggesting that Andean mountains act as a barrier, they found no evidence of bottlenecks, and the relatively

small differences between the populations cast doubt on the morphologically proposed subspecies separation. Eizirik et al. (2008) conducted an updated review of jaguar conservation genetics, concluding that information was still scarce, and that while initial studies had assessed geographic differentiation among individuals on a continental or sub-continental scale, little had been accomplished as far as investigating regional or local jaguar populations.

In the context of gene flow into recent times (and scant evidence for major historic-geographic differentiation), Rabinowitz and Zeller (2010) conducted a range-wide least-cost dispersal connectivity analysis to identify potential corridors connecting known populations and predicting travel routes between them. Due to potential errors in remotely-sensed data and model uncertainties, all the predicted corridors merit and require field validation before conservation actions are taken, with an example of novel corridor assessment being the interview-based occupancy modeling of a predicted corridor in Nicaragua (Zeller et al. 2011; refer to interview-based occupancy modeling section above).

The resources for assessing connectivity and spatial-demographic trends on a large landscape level also include genetic tools. Amato et al. (2008) present a field manual for the collection, storage, and transportation of biomaterials for genetic studies on felids. Collecting scats from nearly the entire country of Belize, Wultsch et al. (2011) emphasize the potentials of molecular scatology/fecal genotyping for understanding connectivity of felid populations.

Natural and anthropogenic boundaries (such as encountered in the NRU) have been shown to affect population dynamics and structure for species with movements at the landscape level. Understanding population boundaries and movement rates can be logistically challenging. Andreasen et al. (2012) used genetic analyses of muscle tissue samples from 739 pumas across the system of relatively moist mountain ranges separated by arid valleys in Nevada and the Sierra Nevada to the west to test the hypothesis that heterogeneous hunting pressure results in source-sink dynamics at the landscape scale. The study found five genetic groups, estimated migration rates among them, and identified the groups as net exporters or net importers (of dispersing individuals). Genetically-effective movement was structured around mountain topography, and large desert basins were an impediment to movement. The most significant asymmetrical movement rates were out of a large area that experienced substantially less hunting pressure, rendering it the largest net exporter (source). The results of this thought-provoking analysis generate interesting insights on the mega-landscape level and the subtleties of the relative weight of habitat quality, prey production, mortality rates, and size of refugia. Although it may be unlikely that genetic jaguar samples can achieve this intensity (the jaguar is a protected species, the puma is a harvested species, and, as Amato et al. (2008) noted, the quantity and quality of DNA recovered in fecal samples is low compared to that recovered from tissue), genetic analyses, including from scats, can contribute significantly to understanding population structure and movement across large landscapes.

Recommendations for Surveying in the Northwestern Recovery Unit

Jaguars and their habitat within the NRU need to be monitored to detect growth or decline in the subunits, both in area (and types) of space occupied and used, and in terms of jaguar numbers and population trends. Based on the logistical challenges and varied terrain and habitat types, a mix of many of the methods described in this document will be necessary.

The monitoring challenges posed by the 226,826 -km² NRU echo those faced in much of jaguar range, where issues of scale, poor access, difficult logistics, and gradients of jaguar and prey abundance require a mix of sampling intensities. The NRU includes extremely rugged terrain in Mexico's Sierra Madre Occidental, low dry forests in hilly areas near the Pacific coast, vast stretches of Sonoran desert, and isolated rugged mountain ranges crossing the international border and scattered throughout the United States portion of the Borderlands Secondary Area (see Figure 1). It is likely different methods will be required for the two core areas (Jalisco 54,949 km² and Sonora 77,710 km²), as compared to the two secondary areas (Sinaloa 31,191 km², Borderlands – Mexico 33,955 km² and United States 29,021 km²), based on cost-benefit ratios.

A cost-effective mix of methods to monitor jaguars and their habitat across core and secondary areas will likely begin with presence and presence-absence spatial approaches emphasizing occupancy for secondary areas. Jaguars are currently scarce in secondary areas, but into which individuals from the core areas may disperse. Abundance studies, which monitor numbers of jaguars, will likely be used within areas where jaguars are more abundant (core areas).

The Sierra Madre Occidental is a priority area for long-term jaguar conservation (Sanderson et al. 2002). Currently little is known about the viability of its current jaguar population or the ability of other areas in the NRU to support jaguars.

A combination of methods will be needed for long-term monitoring of NRU jaguar population trends in space and time (Rosas-Rosas and Bender 2012). In the Sonora core area, low jaguar densities and difficult field conditions urge the use of sign surveys complemented by interviews (which rely on local expertise), judicious placement of camera traps for presence-absence studies, and, where status merits, capture-recapture studies to gauge population size. Farther south, in the Jalisco core area, where the development of large-scale tourism facilities and infrastructure (roads and highways) have caused habitat fragmentation (Nuñez Perez 2007), the remnant jaguar core populations merit intensive studies. Secondary areas (i.e., the Borderlands secondary area and Sinaloa secondary area) merit ambitious presence-absence surveys with covariates which can help inform management needs.

In addition, it is crucial to develop environmental education and wildlife enterprises based on strategies that provide incentive-driven conservation, because this type of conservation promotes coexistence between landowners and jaguars (Rosas-Rosas and Valdez 2010). Jaguar attacks on livestock jeopardize recovery by generating suspicion and intolerance. Engaging landowners in

proactive ways that benefit them and generate interest may not only reduce the frequency of attacks, but also reduce the numbers of jaguars killed for their perceived or real role in livestock losses (Rosas-Rosas et al. 2008, Rosas-Rosas and Bender 2012).

Ecological and management considerations to reduce conflicts are presented in Appendix 2.

Summary and Closing Remarks

Jaguar conservation success in the NRU will depend upon execution of a comprehensive bi-national approach that applies a bi-national metapopulation perspective to recovery. Due to the limits of historical data, we do not know if jaguars were continuously distributed across the entire area in historical times. More likely, due to natural habitat gradients of prey and cover, the NRU contained a natural metapopulation with subunits separated by intervening unsuitable areas and dispersal providing connection between them. If so, that system of habitat islands and intervening areas successfully supported jaguars across a wide area. Today, suitable jaguar habitat remains, yet much of it now lacks jaguars. It is likely that livestock losses and associated perceptions, attitudes, and practices drove much of the well-documented range retraction. Road construction, human population growth, and habitat loss and conversion have played a large role in reducing the jaguar's range in the NRU.

In 2013, jaguar populations were so fragmented in this 226,826 km^2 area that, in much of it, they cannot even be considered a population, simply occasional dispersing animals. Yet, with a wealth of wild, rugged terrain, possibilities of improved game (prey) management, and increased interest in and appreciation for jaguars, there are enormous potentials for recovery in the NRU. Human presence and infrastructure has greatly increased in the last century, which presents additional challenges for maintaining core populations and accomplishing recovery across areas now either sporadically occupied, or vacant, yet with potential. That said, attitudes toward jaguars and jaguar conservation have changed significantly in recent years, giving a glimmer of hope to the future of jaguars.

The potentials for recovery have been demonstrated by the recent documentations of jaguars that have ventured into areas where they had been eradicated, found suitable habitat and sustenance, and survived. Dispersal (through corridors, planned or otherwise) and occupancy in strongholds (large or small) can combine for a system in which immigration compensates for local declines, and even patch extinctions. Small subpopulations can become re-established, which, with enough of them, could become an active metapopulation that spans the international border.

This requires a coordinated approach, which includes the application of effective outreach to improve attitudes and modify agricultural practices, collaborations with development interests to design an effective jaguar conservation landscape, improved wildlife management throughout the recovery unit, and applying a cost effective monitoring system to measure success, as well as aspects in need of improvement.

In this document we have presented the basics of jaguar monitoring. Our introduction includes a review of survey design and statistical analyses, which includes distribution mapping, presence, presence-absence, occupancy, density estimates, abundance indices, and measurements of trends. This is followed by reviews of the use of field sign, interviews, remote cameras, hair traps, scat dogs, and capture and telemetry as monitoring techniques. This entire gradient of methods is relevant to the NRU.

Monitoring intensity should vary along gradients according to status and security of jaguars in subunits. Monitoring vital rates in core areas and tracking dispersal from them would increase understanding of jaguar needs in the NRU. On the other end of the spectrum, along the margins of the recovery unit and in the unsuitable areas separating richer patches, finding evidence of jaguars will be challenging, but can be addressed. The initial challenge will be to determine cost-effective, area-expansive, sustainable monitoring tools that can indicate trends.

Understanding how to conserve jaguars and monitor the effects of management actions and the overall status of jaguars has come a long way in recent decades. In its fragmentation and gradients, the NRU resembles much of the jaguar's range of today and the future. The combination of core and secondary areas presents the challenge of working with human interests to maximize conservation of core areas and the connections between them, and also provides a critical opportunity to design long-term large scale jaguar monitoring.

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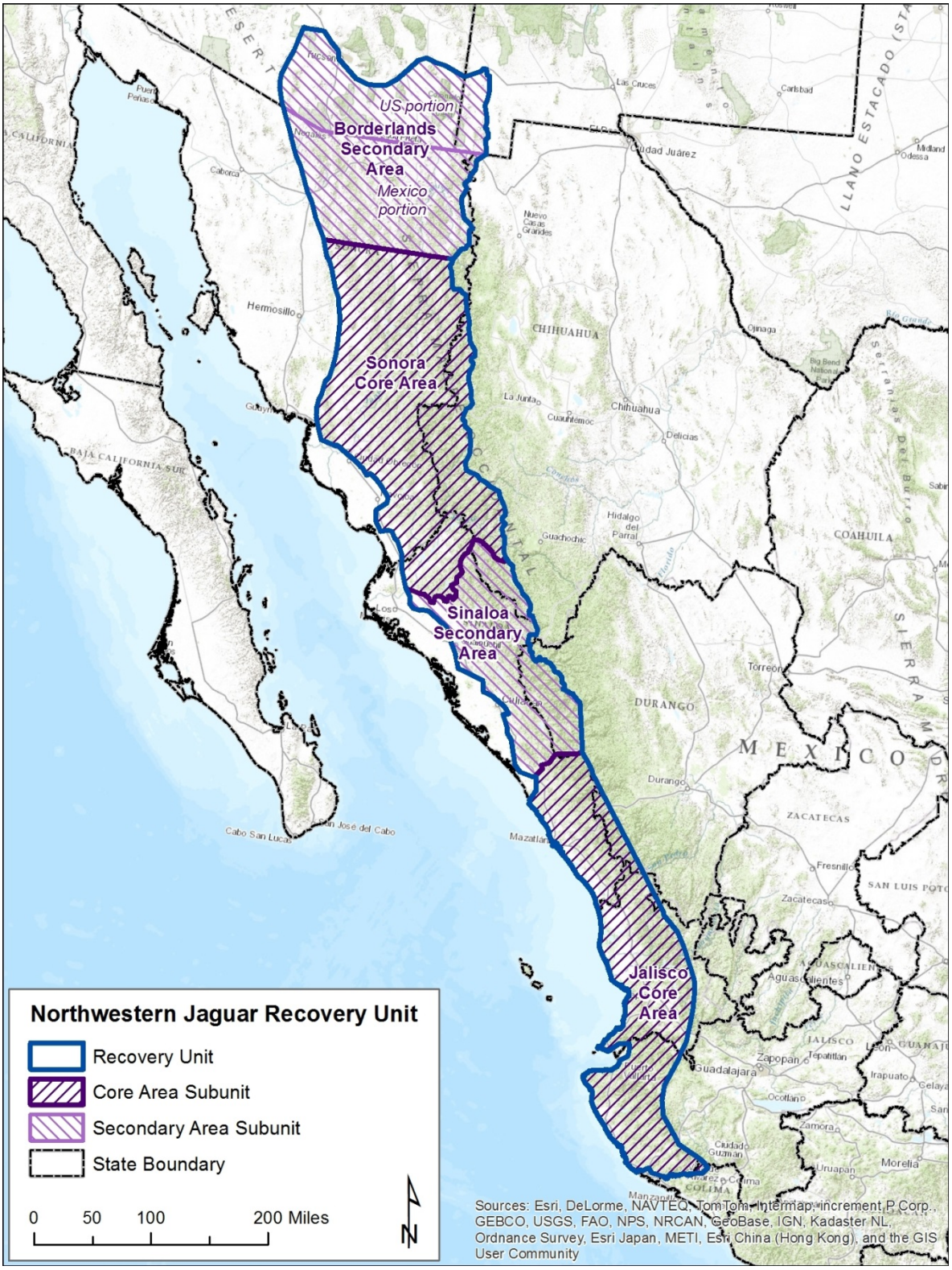

Figure 1. The 226,826 km² Northwestern Jaguar Recovery Unit (NRU) straddles the United States-Mexico border with approximately 29,021 km² in the United States and 197,805 km² in Mexico.

Appendix 1:
Jaguar Capturing and Handling

Background

The first generation of jaguar studies that involved physical captures and radio-tracking was led by George Schaller, Peter Crawshaw, and Howard Quigley in the Pantanal of Brazil (Schaller and Crawshaw 1980, Quigley 1987, Crawshaw and Quigley 1991, Quigley and Crawshaw 1992), Alan Rabinowitz in Belize (Rabinowitz 1986*a*, Rabinowitz and Nottingham 1986), and Louise Emmons in Peru (Emmons 1987). Mondolfi and Hoogesteijn's (1982) observations on jaguars in Venezuela also included information on capture methods.

In the 1990s, Crawshaw (1992) and Hoogesteijn and Boede (1992) presented capture and immobilization recommendations in the edited volume *Felinos of Venezuela*. Hoogesteijn and Mondolfi's (1992) book, *The Jaguar*, summarized many of the first generation of studies, also providing first-hand information on capture methods based on experiences in the high plains of Venezuela. Crawshaw's (1995) studies in Iguazu in Brazil provided a training ground for some of Brazil's leading jaguar biologists of today.

Entering the second millennium, Ceballos et al. (2002), Morato et al. (2002), Nuñez et al. (2002), and Scognamillo et al. (2002) included information on capture methods in research papers in the edited volume *El Jaguar en el Nuevo Milenio* produced by the National University of Mexico and the Wildlife Conservation Society (Medellin et al. 2001). Deem (2002), Deem and Karesh (2005), McBride Jr and McBride (2007), and Furtado et al. (2008) presented observations and recommendations for capture, immobilization, and handling. Ecological research involving jaguar captures includes the works of Polisar et al. (2003), Scognamillo et al. (2003), Silveira (2004), Soisalo and Cavalcanti (2006), Azevedo and Murray (2007*a*, *b*), Cullen Jr (2007), Cavalcanti and Gese (2009, 2010), and Ramalho (2012).

The summary provided in the following section draws upon the above listed body of work and has been augmented by puma literature rich in relevant methods (e.g., Hornocker 1970; Seidensticker et al. 1973; Hemker et al. 1984; Logan et al. 1986, 1999; Lindzey et al. 1992; Ross and Jalkotzy 1992; Beier 1995; Davis et al. 1996; Maehr 1997; Logan and Sweanor 2001; Anderson Jr and Lindzey 2005; Shaw et al. 2007; Knopff et al. 2009, 2010; Ruth et al. 2010; Hornocker and Negri 2010; Elbroch and Wittmer 2012, 2013). Relevant articles can also be found in the literature on Asian tigers, African lions, leopards, and snow leopards.

Capture Methods

All capture methods for research entail some risk for the target animal, with the potential for injuries and physiological stress. Factors to consider when selecting capture methods include: 1) what access does the method require; 2) how portable is the method; and 3) how selective (and thus efficient) is the method. To-date, trained hounds, foot snares, and box/cage traps have been employed to capture jaguars. The following section provides an overview of these methods.

Deem (2002) provided veterinarian guidance to minimize risk in capture and immobilization of free-living jaguars, which was expanded in the WCS Jaguar Health Program manual (Deem and Karesh 2005). Both references suggest that capture teams include an expert veterinarian. Jaguar research references that describe captures and delivery of immobilizing agents (summarized in more detail below) include Azevedo and Murray (2007 b), Cavalcanti and Gese 2010), Crawshaw (1992), Furtado et al. (2008), Hoogesteijn and Boede (1992), Hoogesteijn and Mondolfi (1992), McBride Jr., and McBride (2007), Morato et al. (2002), Nuñez (2006), Quigley (1987), Rabinowitz and Nottinham (2006), and Scognamillo et al.(2003). Another useful reference is the Guidelines of the American Society of Mammalogists (Gannon et al. 2007, Sikes et al. 2011).

Hounds

The use of trained hounds to capture jaguars for research has a long history and high rate of success (e.g., Schaller and Crawshaw 1980, Quigley 1987, Crawshaw and Quigley 1991, Quigley and Crawshaw 1992, Polisar et al. 2003, Scognamillo et al. 2003, Silveira 2004, Soisalo and Cavalcanti 2006, Azevedo and Murray 2007*b*, McBride Jr and McBride 2007, Furtado et al. 2008, Cavalcanti and Gese 2009), as well as successful use with pumas (Hornocker 1970; Seidensticker et al. 1973; Hemker et al. 1984; Ross and Jalkotzy 1992; Lindzey et al. 1992; Davis et al. 1996; Maehr 1997; Anderson Jr and Lindzey 2005; Shaw et al. 2007; Knopff et al. 2009, 2010; Ruth et al. 2010; Hornocker and Negri 2010; Elbroch and Wittmer 2012, 2013).

Among the advantages of using hounds is rapid selective captures, usually within hours of finding a fresh scent. Efficient terrestrial travel routes, which cut across terrain where tracks can be located, elevate that efficiency (e.g., dirt roads). Even where travel logistics are challenging, such as with the classic puma studies in remote, mountainous areas in central Idaho (Hornocker 1970, Seidensticker et al. 1973), hound captures are far more efficient than box/cage traps.

Captures with dogs carry some risks of mechanical injuries and physiological stress of pursuit to the target animal, as well as confrontations between the dogs and cats which may result in injuries or death. Logan et al. (1999) cites deaths of pumas during dog captures of 3.7%, 4.6%, and 8% of puma captures in Idaho, Colorado, and Utah respectively (Hornocker 1970, Anderson et al. 1992, and Lindzey at al. 1989). However, Ross and Jalkotzy (1992) in Alberta captured 68 pumas 129 times with zero mortality using hounds. McBride Jr and McBride (2007) describe hunting with hounds, security and safety, equipment, tranquilizing, and capture and handling scenarios in a semi-xeric habitat with low vegetation, reporting zero mortality and injury during 15 jaguar captures and 4 recaptures in the Chaco of Paraguay. Their paper presents rare details on capture methods and a number of experience-based capture and handling tips to minimize stress and injuries, including the recommendation that all captures be conducted during cooler months. Furtado et al. (2008) describe jaguar captures with hounds, and Shaw et al. (2007) provide guidance for puma captures. Davis et al. (1996) designed a device to safely remove

immobilized pumas from trees and cliffs. In summary, captures with hounds can be selective and rapid, especially where one can rapidly cross cat trails/tracks.

Snares

The use of foot snares as a jaguar capture technique is still on the learning curve, borrowing from examples with pumas (Logan et al. 1999, Shaw et al. 2007), snow leopards (McCarthy et al. 2005), and Siberian tigers (Goodrich et al. 2001, 2010). The lightweight portability of snares is an appeal in exceptionally remote sites. Modified foot-hold snares have been employed for jaguars in Belize (Figueroa in progress), western Mexico (Nuñez 2006) and in the upper Amazon of Peru (Furtado et al. 2008) and flooded forest of the Brazilian Amazon (Ramalho 2012). Nuñez (2006) used Aldrich foot snares to capture 9 jaguars with no lesions or injuries. Seventeen jaguars were captured with no serious injuries or cuts in the Peruvian Amazon using snare methods described in Furtado et al. (2008). The authors caution against setting snares where capture probabilities of non-target species are high, and urge frequent trap checks (e.g., 2 x per day—echoed by Goodrich et al. (2001) for tigers) or monitoring the trap with telemetry, such as recommended by Nolan et al. (1984) for grizzly bear snares.

Logan et al. (1999) deployed this method for pumas in a xeric habitat where trees were scarce, thereby reducing options for cats followed by hounds to tree and elevating probabilities that they would bay on the ground, potentially increasing dog or cat injuries or mortality. Elevated body temperatures during chases, and falls from trees or cliffs, are additional factors that might urge using snares rather than hounds in mountainous, hot areas. The evolution of effective designs, deployment, and capture considerations for snares are described in Logan et al. (1999) and elaborated upon in Shaw et al. (2007). Any trapping method (including snares) is less rapid than dogs following fresh scent. Snares do carry risks of injuries, with the largest concern being impeded circulation to the paw in the snare, as well as physical abrasions to the lower limb or paw, especially if the animal is lunging at the researchers. Goodrich et al. (2001) report foot swelling in snared Siberian tigers as 39% low, 28% medium, and 33% high. One tiger wore a canine nearly through on snare cable, and another, captured by the hind leg, suffered a severe laceration and broken metatarsals. Goodrich et al. (2001) considered the snares to be effective, even if effort per capture was high, with the lightweight portability of snares providing an advantage in remote roadless areas. Administering drugs as quickly as possible and backing off reduces animal stress and injuries.

The proportional risk of snares has not yet been outlined in the jaguar literature, as the use of snares for jaguars is relatively recent. Thus far, researchers report satisfaction and success. Ramalho (2012) used snares during low water periods in Varzea forest in the Brazilian Amazon. Working in Central Belize, Figueroa (personal communication) learned snare techniques from an experienced puma trapper and an experienced leopard trapper, then, frustrated with the inefficiencies of these techniques when applied to trapping jaguars, refined his methods for increased effectiveness. Although the details of some of the recent efforts with snares with

jaguars are forthcoming, the method has been used with other large cats, and preliminary results with jaguars suggest that, when snares are designed to minimize injury and are checked frequently, they provide a lightweight, portable, and effective trapping method.

The recommendations to minimize possibilities for physical injury contained in Logan et al. (1999) and Shaw et al. (2007) should be studiously followed when using snares to maximize efficiency and minimize trauma to study animals. Logan et al. (1999) and Shaw et al. (2007) cover the risks on injury and the innovations developed to minimize them. Veterinarian guidance provided by Deem (2002) and Deem and Karesh (2005), as well as veterinarian expertise in capture teams, is critical to minimize the opportunity that small abrasions incurred during any capture method later become large infections. The capture of non-target species represents a great inefficiency of lost time and can damage a cable snare, so must be minimized. Guidance is presented in Logan et al. (1999), Shaw et al. (2007), and Furtado et al. (2008).

Box Traps

As with snares, box/cage traps baited with live animals involve waiting for a capture, whereas dogs entail going to the cat, which is more efficient. As noted by researchers working in remote areas of Siberia (Goodrich et al. 2001), baited cage/box traps can be ineffective for captures away from human habitations, are too unwieldy to use in remote areas, and may result in injuries such as broken teeth (Rabinowitz 1986*b*). In numerous study areas, access, logistics, and efficacy recommend against baited box traps or cage traps. That said, they have been used by Rabinowitz (1986), Morato et al. (2002), and Azevedo and Murray (2007*a*), and have contributed to our knowledge of jaguars. Construction that minimizes opportunities for injuries and access that allows deployment of this relatively cumbersome method are paramount considerations (Furtado et al. 2008). Crawshaw (1992) provides guidance to reduce injuries when constructing box traps. Hoogesteijn and Mondolfi (1992) provide descriptions and photographs of cage captures.

Immobilization and Handling

The era of powder driven Palmer Capchur rifles and homemade jab sticks to deliver immobilizing agents has given way to lighter weight CO^2 and air powered products that, albeit expensive, deliver immobilization agents while minimizing risk to the animals.

Telinject offers lightweight CO^2 and compressed air rifles, CO^2 and compressed air pistols, blowpipe "remote injection systems," darts, and accessories (http://www.telinject.com/catalogue/). Daninject offers CO^2 powered rifles and pistols, blow pipes, jab sticks, darts, and accessories (http://www.dan-inject.com/all/Page-2.html). Pneu-dart offers CO^2 powered rifles and pistols, blow pipes, darts, and accessories (http://www.pneudart.com/). These "remote drug delivery systems" (RDDS) need to be augmented by a readily available range of sizes of syringes and a selection of needles (including wide [e.g., 18 gauge] needles) for post-capture injections and contingencies. It is recommended to have two RDDS on hand (e.g., a rifle and a pistol) in case one gets damaged. Rifles deliver the

drugs effectively at longer distances, which can reduce animal stress. Jabsticks work well with snared animals and provide the advantage of instantly understanding how completely the drug was delivered, but carry the risk of greater stress for the animal due to human proximity during the delivery (e.g., straining against a snare). For treed cats and in rocky terrain, the confidence and distance that a good rifle system provides is significant.

In the WCS Jaguar Health Manual, Deem and Karesh (2005) provide guidance on dart placement and dosage calculation, as well as recommendations for immobilizing agents (e.g., telazol, ketamine, xylazine) and safety considerations. The manual includes a review of drugs used on captive jaguars and a literature review of those used with free-ranging jaguars: ketamine (Rabinowitz and Nottingham 1986, Crawshaw 1992, Hoogesteijn and Mondolfi 1993), ketamine and diazepam (Hoogesteijn and Mondolfi 1993), ketamine and xylazine (Quigley 1987, Hoogesteijn and Mondolfi 1993), and telazol (Crawshaw 1992, Hoogesteijn and Mondolfi 1993, Morato et al. 2002). Also discussed are supplemental drugs delivered during handling, drug interactions, and supportive medications. The manual provides detailed advice for handling jaguars, monitoring their vital signs during handling, trouble-shooting emergencies (from mild to extreme), and how to collect biological samples. Gannon et al. (2007) provide guidelines for research on wild mammals. Kreeger and Arnemo's (2012) handbook of wildlife chemical immobilization provides a general reference for these techniques.

Scognamillo et al. (2003) used Telinject rifles, a medetomidine and ketamine mixture, and atipamezole as a reverter (antagonist). Azevedo and Murray (2007*a*) used a Brazilian brand of drug called Zoletil, a compound of Tiletamine hydrochloride and Zolazepam hydrochloride similar to Telazol. McBride Jr and McBride (2007) preferred a ketamine-xylazine mix for safety and predictability, and considered medetomodine-ketamine combinations unsafe and unpredictable. Cavalcanti and Gese (2010) used Telazol, or a Telazol and ketamine combination, delivered with a dart from CO^2 pistol or rifle.

Ross and Jalkotzy (1992) had success with 68 treed pumas in mountainous terrain in Alberta using a combination of ketamine and xylazine. Goodrich et al. (2001) describe successful capture and handling procedures for Siberian tigers using a mix of ketamine and xylazine delivered to snared tigers with Telinject dart guns or blow guns. Goodrich et al. (2001) also provide details of capture experiences, including handling several types of emergencies (including the use of Diazepam to stop seizures). The size of Siberian tigers required two darts for full dosage, unlike jaguars, which are about one-half the size. McCarthy et al. (2005) used Telazol delivered to snared snow leopards with a jab stick. Knopff et al. (2010) captured 9 pumas using a dart gun delivering a ketamine and medetomidine mixture, and 44 using a Telazol-xylazine mix. Ruth et al. (2010) used hounds and ketamine and xylaxine to capture pumas in Yellowstone National Park. Elbroch and Wittmer (2012) delivered ketamine with a dart gun and Zalopine with syringe once immobilized. The Puma Field Guide by Shaw et al. (2007) provides guidance on darting pumas and handling pumas, stating that barbed or collared darts delivered with compressed air injection systems are probably the safest.

In summary, hounds are efficient, but when not available, snares are effective. A variety of immobilizing agents have been tried, with considerable successful use of ketamine and xylazine for both jaguars and pumas, particularly when the animal is in a tree.

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Appendix 2:
Ecological Factors in
Human-Jaguar Conflicts and Coexistence

This appendix presents management considerations to reduce conflicts between livestock and jaguars in an ecological context. The ecological/behavioral factors of jaguars that contribute to conflicts include: prey selection, learned behaviors, and habitat selection patterns. These factors provide the foundation for the management practices that are suggested below to reduce the frequency of conflicts.

Foundations

Prey Selection

An understanding of jaguar prey selection helps lead to an understanding of some of the factors that can lead to attacks on livestock. In the remote and nearly pristine upper Amazon rain forest in Peru, Emmons (1987) found jaguars (*Panthera onca*) taking most prey in proportion to their abundance, with the exception of collared peccaries (*Pecari tajacu*), which were taken in higher proportions, suggesting preference for this larger bodied prey item. In the heavily forested Cockscomb Basin in Belize, Weckel et al. (2006) found jaguars opportunistically taking many prey items in proportion to availability, although they took collared peccary in greater proportions than available and tapirs (*Tapirus bairdi*) and white-lipped peccaries (*Tayassu pecari*) less than expected. The authors speculated that the massive handling cost of tapirs could be the reason they were taken at a lower proportion than available, but were puzzled about the reticence to take white-lipped peccaries, which are a preferred prey item in several other locales. The proportion of white-lipped peccaries in jaguar diet in the Cockscomb increased following a complete hunting ban, but the relative occurrence of armadillos, a small prey item in the diet, stayed relatively constant after the ban (51% after 20 years of formal protection vs. 54% before (Foster et al. 2010*b*)). Belize Cockscomb Basin jaguars (Rabinowitz and Nottingham 1986; male mean = 57.2 kg) were about one-half the size of jaguars in some other regions (llanos Venezuela = 104.5 kg, Pantanal Brazil = 99.5 kg (Hoogesteijn and Mondolfi 1996), and Paraguay = 91.8 kg (McBride 2009)), which might play a factor. Mean weight of vertebrate prey, an index of prey size, was 7.1 kg in the Cockscomb (Foster et al. 2010*b*) and 17.2 kg in the llanos of Venezuela (Scognamillo et al. 2003).

Carrillo et al. (2009) reported white-lipped peccaries and marine turtles being preferred prey in Corcovado National Park in Costa Rica, which suggests prey body size and ease of capture (respectively) as factors contributing to prey selection. In general, when patchily distributed larger-bodied prey are encountered and can be taken without risk, jaguars will show some selection for them. In the horizontally heterogenous savanna-forest mosaics of the llanos of Venezuela, where natural prey occurred in patches related to habitat and resources, jaguars selected for capybara (*Hydrochaeris hydrochaeris*) and collared peccaries, taking white-lipped

peccaries in proportion to availability, and ignoring some small prey items that constituted the majority of jaguar diet in the Cockscomb of Belize (Polisar et al. 2003, Scognamillo et al. 2003). Similar patterns were encountered by Azevedo and Murray (2007*a*) and Cavalcanti and Gese (2010) in the Pantanal of Brazil. Azevado and Murray (2007*a*) found jaguars did not hunt randomly, but consumed larger- and medium-sized prey species more than available. In an area where jaguars and cattle intermingled, Cavalcanti and Gese (2010) recorded cattle, caiman (*Caiman crocodilus*), peccaries, feral hogs (*Sus scrofa*), marsh deer (*Blastocerus dichotomus*), giant anteaters (*Myrmecophaga tridactyla*) , capybara, and brocket deer (*Mazama americana* and *M. gouazoubira*) among the most frequent jaguar kills encountered.

Jaguar diet in homogenous habitats appears to be more opportunistic than in patchy habitats with clumped prey, where jaguars do not capture every prey item encountered. When given the luxury of selection, jaguars will tend to pick medium- and larger-sized prey items. If cattle are in jaguar habitat, they may become part of that equation.

Learned behaviors

Solitary felids can demonstrate individual patterns of food selection. Taking certain prey species appears in part to be a learned skill. Cats will only learn how to take domestic animals if the opportunity presents itself. Once they have acquired the knowledge, some may repeatedly take livestock. Variation in diet among the population occurs even with some natural prey, with prey vulnerability playing a role. Knopff et al. (2010) recorded considerable variation in prey preferences by pumas (*Puma concolor*) in Alberta's Rocky Mountains. Females subsisted mostly on deer (*Odocoileu*s spp.). Adult males killed more large ungulates, including moose (*Alces alces*), adult females focused predation on small ungulates, and sub-adults used the highest proportion of smaller, non-ungulate prey. Female ungulates had a higher representation in the diet in the spring due to pre- and post-parturition vulnerability, while in the fall the proportion of male deer in the diet escalated due to their vulnerability during the autumn rut (Knopff et al. 2010).

Among five intensively monitored female pumas in Alberta, Canada, two never killed bighorn sheep (*Ovis canadensis*), one killed one sheep, one killed five, and one killed 17 in one year (Ross et al. 1997), with this specialization by one animal nearly eradicating the sheep herd.

Monitoring 10 pumas in Chilean Patagonia, Elbroch and Wittmer (2013) found differences in prey selection at the population level and the individual level, with prey including guanacos (*Lama guanicoe*), European hares (*Lepus europaeus*), huemul (*Hippocampus bisculus*), and domestic sheep (*Ovis aries*). Of 10 pumas studied, 2 individuals selected domestic sheep. The effect of these 2 pumas alone was substantial enough to influence the overall dietary preferences of the puma population. In the study area and at a population level, pumas depredated sheep 3.8 times more than expected given their abundance (Elbroch and Wittmer 2013). Similar to the study by Ross et al. (1997), where one puma nearly eradicated a bighorn sheep herd, the effect

on livestock, one or two pumas selecting and/or specializing in sheep or calves can seem acute to a livestock owner, and the retaliation on the puma population can be potentially severe (Polisar 2000).

During a three year study in Venezuela, Polisar et al. (2003) and Scognamillo et al. (2003) noticed that while 1 puma with a radio collar used wild habitats and wild prey exclusively, an uncollared individual within the same area became habituated to calves (or selected for the energetically efficient prey of young calves in maternity pastures) until she was subject to lethal control. During this same study, jaguar attacks on cattle and horses were isolated, infrequent events, and generated no retaliation. In previous years, however, several jaguars had followed a similar path as the puma referenced above, with their recurrent attacks on livestock disrupting ranching operations. This resulted in these individuals being lethally removed, as the patience of the conservation-oriented rancher affected by these depredations was finally exhausted.

Intensively monitoring 10 jaguars and identifying their kills in the Pantanal of Brazil, Cavalcanti and Gese (2010) found that cattle accounted for greater than 50% of the kills for some jaguars, while for other jaguars the proportion was less than 5%. Although this suggests that all jaguars used cattle as food in that study area, the difference in number of cattle killed per jaguar may be significant from a management standpoint.

Hoogesteijn and Mondolfi (1992) recorded previous severe wounds in 53% of jaguars killed to control cattle predation in Venezuela. Rabinowitz (1986*b*) found old shotgun wounds in 75% of jaguars that had attacked cattle in Belize. Both of these studies indicate that wounded jaguars may increase predation on cattle due to the ease of capturing this prey. However, every radio collared jaguar that preyed on cattle in the study area of Cavalvanti and Gese (2010) was in excellent physical condition at time of capture. This follows Polisar's accumulated anecdotal information across virtually all of Mesoamerica and a substantial sliver of South America: sometimes the jaguars preying on cattle are healthy, strong specimens. Had they never been presented with the opportunity to learn to take livestock, specialization would not have become an option, and the lethal control it stimulated could have been avoided.

Habitat selection

Jaguar habitat patterns can be instructive on where to locate livestock to minimize encounters with jaguars. Soto-Shoender and Guiliano (2011) found landscape structure, including forest cover and distance to forest, as the best explanation of the probability of jaguar predation on livestock.

Using telemetry in Venezuela, Scognamillo et al. (2003) found jaguars using habitats (flooding savannas, dry forest, dry savanna with chaparro, semi-deciduous forest, dry pasture, evergreen forest) in the same proportion as available within their home range, with pumas showing a slight selection for open habitats. Also in Venezuela, Polisar et al. (2008) found that in their study area's largest block of semi-deciduous forest of several thousand hectares where natural prey

was abundant, the frequency of jaguar sign on transects and in images collected by camera traps was greater than puma, even though the latter were twice as abundant in the study area. In forest patches 300 ha or larger, 83% and 81% of jaguar and puma locations, respectively, were within the band 0-500 m from the edge, while only 17% of jaguar and 9% of puma locations were in the interior (greater than 500 m from the edge). They concluded that productive ecotones that were productive for prey were not avoided, but rather preferred, as demonstrated by caiman and capybara taken by jaguars in low stature secondary growth, the primary attraction of which was prey, adjacent water, and the low vegetation next to it.

In an area in the Pantanal where livestock mortality due to predation was low, Azevedo and Murray (2007*b*) reported that forest proximity was the only factor explaining livestock mortality, with predation risk increasing as distance to forest cover declined, but predation risk was highest for calves, declining for yearlings, and even lower for adults. Using locations from 10 radio-collared jaguars in the south Pantanal, Cavalcanti (2008) found forest and shrubland used more than their availability, and open field, with or without trees, and bare agricultural land generally avoided by jaguars. Herbaceous field and drainage vegetation were avoided during the wet season, but used according to availability during the dry season. Of 6 radio-collared male jaguars, forest habitats were preferred by 5. Three of 4 female jaguars used forest habitats in proportion to availability. Shrub-like habitats were selected by 7 of the 10 collared jaguars and open field avoided by 9 of the 10 (Cavalcanti 2008). Almost half of 392 located jaguar kills were found in shrubland, and kills in both forest and open areas occurred in proportion to that habitat's availability.

The conclusion of all the preceding citations is jaguars generally prefer forest and shrub-like habitats, but kills can easily be made along ecotones, and hunting cover need not be mature forest. As Azevedo and Murray (2007*b*) found, maintaining livestock in or near hunting cover for jaguars (which can be shrubs, high grass, or forest edge) leads to increased livestock mortality risk. Ranch designs that separate livestock from jaguar habitat will minimize opportunities for jaguars to consider livestock as prey options and learn to take them.

Foraging theory and management recommendations

Prey search costs and the relative availability of potential foods play a role in livestock consumption by jaguars. The value of patches of wild prey is reduced through increased fear and vigilance of prey following attacks by predators (Brown et al. 1999). As a result, prey can become temporarily marginal (Charnov 1976), driving up search and pursuit costs for predators (as outlined in the optimal foraging theory by MacArthur and Pianka 1966) and explaining why jaguar home ranges are large enough to include multiple patches of nutritious prey. A hunting activity (search and pursuit of a prey item relative to other prey) will be expanded as long as the resulting gain in time spent per unit food exceeds the loss (MacArthur and Pianka 1966). Prey preference is expressed by the relationship between absolute and relative abundance of all potential foods, and the proportion of that food in the diet (Emlen 1966). Animals cannot afford

to be selective when resources are scarce, and selectivity increases with overall food density (Emlen 1966), which relates to both the allure of livestock in prey-depleted environments, and also to the energetic boon that relatively immobile and defenseless calves represent in comparison to other species, such as mobile, tusked peccaries and semi-aquatic caiman.

In temperate regions, black bears (*Ursus americanus*) reliance on anthropogenic food sources increases when natural food production falters. Using a foraging theory approach, Baruch-Mordo (2013) modeled increases in costs and reductions in benefits. Reductions in anthropogenic food sources in urban and urban-interface patches did not eliminate their use by bears with extremely low fat reserves, but overall, on a population level, selection of urban patches decreased. Similarly, the relative availability of natural and wild prey plays a role in the diet of jaguars. Amador-Alcala et al. (2013) found predation on livestock negatively related to prey abundance in the jungles of southeastern Mexico. In the Pantanal, Calvalcanti and Gese (2010) found that the kill rate of cattle was inversely related to the availability and consumption of peccaries and caiman.

The prevailing cattle management practices in the south Pantanal caused Cavalcanti and Gese (2010) to consider cattle an inevitable part of jaguar diets, justifying accommodation of this depredation through compensation to ranchers. That may be the ecological and social reality in that area (and others). However, any scenario in which some livestock will be available to support jaguars should be avoided, as it leads to learned behaviors (covered above). The goal of never allowing jaguars to learn to take livestock in the first place is immensely challenging, but worthwhile.

The management lessons from foraging theory are the following: 1) preserving the option of natural prey can help prevent jaguars from depredating cattle and pigs by minimizing the energetic search costs for jaguars to locate adequate natural prey, and 2) domestic animals are low search cost and energy rich food items, so maximizing the search costs for jaguars by minimizing and even impeding their access to livestock is important.

Appropriate livestock management can significantly reduce livestock depredation by jaguars. That said, even with good livestock-management practices and healthy jaguars, human-jaguar conflicts are inevitable. In some instances, lethal control of jaguars may be the outcome of a human-jaguar conflict, but reducing the frequency of attacks on livestock by avoiding opportunities for depredation by jaguars is a worthy goal, and can help effect jaguar conservation.

Conservation Concepts

Killing by humans, a primary factor in the jaguars' approximately 50% range retraction in the last 100 years, has been intrinsically related to the expansion of human habitations and agriculture into jaguar habitat. These range from small indigenous villages in forests to huge cattle ranches. That trend continues today, as ranches and farms penetrate jaguar habitat and in

their design (or lack of) generate conflicts and further fragmentation and retraction of jaguar range. Jaguars have been killed due to their association with losses of cattle, pigs, sheep, and dogs throughout their range. That said, it is often the rancher and farmer who lives on the edge of jaguar habitat and whose perspective and practices may be instrumental in effecting human-jaguar coexistence.

Significant conservation advances include: 1) protected areas and biosphere reserves that have been set aside to effect species conservation, and 2) an increased understanding of the factors contributing to jaguar attacks on livestock. There are two primary components to managing the issue of jaguar attacks on livestock: one is to limit the options for cats to become familiar with the nutritional qualities of domestic animals, the other is to manage the issues surrounding jaguars that have become habituated to domestic prey.

Losses of livestock to carnivores can be substantial in economic terms. Sommers et al. (2010) quantified the economic impact of grizzly bear (*Ursus arctos*) and gray wolf (*Canis lupus*) depredation on calves in an area of western Wyoming, U.S. An increase in calf losses coincided with grizzly bear and gray wolf arrival (as each species began to recover and expand its range), starting with grizzly bears in 1995 and wolves in 2000. Between 1995 and 2004, 29,693 calves were grazed in the area, and, of 1,332 lost to all causes, an estimated 520 were lost to grizzly bears and 177 to gray wolves. The monetary value of losses attributable over a 10-year period was $148,000 to grizzly bears. The take home message is that livestock losses to carnivores have real value. Engaging effectively with ranchers in meaningful ways is important for jaguar conservation to maintain their support. Strategies for that engagement include ecotourism, with examples from the Pantanal of Brazil (Hoogesteijn and Hoogesteijn 2011), trophy deer hunting in Sonora that provided an added value for wildlife to compensate for possible cattle losses to jaguars (Rosas-Rosas and Valdez 2010), and technical assistance (livestock nutrition and watering technologies) in Guatemala (Polisar personal commmunication).

Robinson et al. (2008) explored effects of puma hunting and removal in a study that is relevant to livestock management in areas that are poor in natural prey, whether intrinsically so, or through overhunting. The authors found that puma removal in prey-productive habitats increased immigration and recruitment of younger animals from adjacent areas, resulting in little or no reduction in local cougar densities, and a shift towards younger animals. In this manner, hunting pumas in high-quality habitat (meaning areas with abundant, easily-accessible prey) may create an attractive sink, where a locally high density of pumas (and high rates of encounters and mortality) can lead to a misinterpretation of larger population status and mask true population trends both in the sink and surrounding less productive areas (Robinson et al. 2008). This phenomena is a real risk when livestock operations are placed in jaguar habitats that formerly harbored smaller wild and mobile prey items. Where bovids (cattle) and equids (horses) are introduced into jaguar habitat with inherently low productivity (and thus prey biomass) or a prey base already reduced through overhunting, high rates of predation on cattle and horses may occur, suggesting a higher density of jaguars than exists. If the management scenario continues,

with livestock placed in poor prey areas, the elements described above of foraging theory, prey selection, and learned behaviors contribute to a cycle of cats learning to take livestock and being controlled as a result.

Landscape design and management of individual ranching operations to minimize opportunities for carnivores to learn to take livestock is an important factor in jaguar conservation.

Interventions to reduce the impact of jaguar attacks on livestock

Field studies and observations have identified the vulnerability of calves to predation (Quigley and Crawshaw 1992, Polisar et al. 2003, Scognamillo et al. 2003, Azevedo and Murray 2007*b*, Hoogesteijn and Hoogesteijn 2011). McBride (2009) noted the positive effects of abundant natural prey and strategically placed waterholes for native prey outside of livestock pastures as methods to reduce the frequency of jaguar attacks on livestock in the central Chaco of Paraguay.

To reduce conflicts between jaguars and livestock, as well as consequent retaliatory killing of jaguars, proactive livestock management actions must be implemented. To accomplish this, education and technical assistance to ranchers and farmers must be provided that: 1) details the methods by which cats can be prevented from learning to take cattle, and 2) enables them to distinguish between those individual cats that are taking livestock with frequency, those that are not, and those that do so on irregular occasions (Marchini et al. 2010, Hoogesteijn and Hoogesteijn 2011).

Below are suggested steps to reduce livestock losses to jaguars that should be included in any rancher outreach efforts.

Interventions to reduce jaguar predation on livestock

Interventions for ranchers to reduce impact of jaguar predation on livestock (Hoogesteijn and Hoogesteijn 2011):

1. Keep a written registry of all livestock losses. Ranch books should include date, place, stage of livestock, and cause of death. This helps with accurate analyses of sources of losses and characteristics of losses actually attributable to jaguars. In addition, take photographs of all cattle suspected to be killed by carnivores.

2. Control hunting, both indiscriminant hunting of jaguars (wounding healthy animals) and their prey (reducing natural alternatives to livestock). Maximize natural prey as a primary food source for jaguars.

3. Use night corrals, lighted pastures, or electric fences for vulnerable stages and species of livestock (calves, pigs, sheep). Leaving vulnerable stages and species in situations where jaguars can take them can initiate the depredation cycle. Make it difficult for this to happen by creating scenarios in which vulnerable livestock such as calves are far from

forest and jaguar travel routes, and accessing the calves has costs to the jaguars (crossing open areas, proximity to humans, powerful electric shocks, disagreeable lights).

4. Locate water sources outside of pastures in seasonally dry habitats to influence the separate distribution of prey and livestock. By placing water (an essential resource for wildlife) outside of pasture areas, wildlife distribution can be affected and productive prey areas can be separated from productive pastures.

5. Keep cattle out of forested areas and away from forest edges. Jaguars will hunt along forest margins, are comfortable with forest-open area ecotones, and, when livestock of any stage are allowed to enter forested areas, an opportunity for jaguars to experiment with a new food source is provided and the depredation cycle may begin (Polisar et al. 2003, Scognamillo et al. 2003, Azevedo and Murray 2007*b*, Soto-Shoender and Giuliano 2011). Keep all cattle, pigs, and sheep out and away from forested areas. In the humid tropics, pigs often are free-roaming, entering the forest at will, with similar results as described above for cattle. Pilot projects enclosing pigs in corrals separate from forest have been delivering promising results in terms of reduced predation in Mesoamerica (Polisar personal observation).

6. Control calving seasons and locations. Calves are one of the most vulnerable prey jaguars can encounter. A calf provides a large amount of food that is essentially defenseless and cannot escape. Thus, the first priority in reducing options for jaguars to learn to take livestock is to control calving seasons and locations by carefully designing and managing maternity pastures to inhibit easy entry by carnivores (Hoogesteijn and Hoogesteijn 2011).

7. Keep older, larger, aggressive, and experienced livestock with younger, more defenseless livestock. This recommendation may not help if a large jaguar has learned to take small livestock and has worked up to any size, but having to contend with larger, more experienced, aggressive livestock has been shown to reduce attacks in pastures where, previously, young animal losses had reached unacceptable levels. Changing types of cattle operations and moving herds in response to high depredation rates, such as placing more aggressive, mature animals in pastures where calves are being lost, can be a deterrent.

8. Use cattle races, such as Pantaneiro and San Martinero, that are resistant to jaguar attacks.

9. Improve overall and reproductive health of livestock to improve production and reduce the relative impact of losses to jaguars (Hoogesteijn and Hoogesteijn 2011).

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Appendix 3:
Glossary

Accuracy: combines both bias and precision in an assessment of estimator performance. An accurate estimator is one that is both unbiased and precise, whereas an inaccurate estimator is either imprecise or biased, or both. An accurate estimate is close to true population value.

*Ad hoc areal estimate*s: have been used to generate density estimates from number estimates when the true sampling area is unknown. In an attempt to generate an estimate of the area that the sampled animals occupy and, thus, a density estimate, the movements of animals recaptured during the study have been used as a parameter related to home range. When the sample grid is large and the home range of the study animals is small, this approach is relatively problem free, as the sample grid eclipses many home ranges and the maximum distances between captures can be averaged as Mean Maximum Distance Moved (MMDM), which provides a buffer to the capture grid for a realistic estimate of the sample area. Under obverse conditions, where home ranges are large relative to the sample grid, MMDM may simply retrieve the limitations imposed by the scale of the grid, resulting in an under-estimate of home ranges (thus area sampled), and if so, a bias which results in an over-estimate of the density of the study animal.

Bayesian Statistical Methods: seek to provide a probabilistic characterization of uncertainty about parameters based on the specific data. Both data and parameters are viewed as random variables according to the calculation known as Bayes' Rule and a probability distribution is generated based on the data, which is referred to as the posterior distribution. Bayes' theorem expresses conditional probability (or "posterior probability") of an event A when B is observed, in terms of the "prior probability" of A, and the "conditional probability" of B, given A.

These methods, which require considerable iterations, have become more popular in recent years due to faster computers and more efficient methods for solving complex Bayesian inference problems. In the Bayesian view, data are realizations of random variables, and the parameters of the model are also random variables.

The Prior distribution, when combined with information about the conditional probability distribution of new data through specified functions, yields the posterior distribution, which in turn can be used for future inferences. A uniform prior distribution is a symmetrical probability distribution in which all intervals (values), continuous or discrete, are equally probable. A discrete uniform distribution is a symmetric probability distribution in which a finite number of values all are equally likely.

Expert opinions can inform "priors" resulting in strong prior distributions, leading to less uncertainty in posterior distributions. The sequential collection of data to specify

transitions from prior probabilities to posterior probabilities is an iterative process that can be time consuming, with posterior probabilities resulting from data collection in one period becoming the prior probabilities for the next period.

Bias: systematic deviation of the estimate from the true parameter of interest.

Confidence interval: is used to gauge the reliability of an estimate. It does not indicate a point value. It is the interval for which repeated analyses would include the true value at the indicated confidence level. For example, a confidence interval between 2 and 20 with a 95% confidence level means that the true value of the parameter being estimated would occur in that band during 95% of the repeated analyses. Using an interval of 8 to 12 with a 95% confidence interval would be more precise. If, however, the sampling includes systematic bias, the results can produce a relatively narrow, yet also inaccurate, confidence interval.

Core areas (U.S. Fish and Wildlife Service 2012): are the areas within a recovery unit for the jaguar with the strongest long-term evidence of jaguar population persistence. Core areas have both persistent, verified records of jaguar occurrence over time and recent evidence of reproduction.

Criteria for core areas:

1) Reliable evidence of long-term historical and current presence of jaguar populations.

2) Recent (within the last 10 years) evidence of reproduction.

3) Contains habitat of the quality and quantity that is known to support jaguar populations and is of sufficient size to contain at least 50 adult jaguars.

Corridor: area connecting protected areas/source sites.

Discrete uniform prior distribution: in Bayesian statistical methods, a prior distribution where a finite number of values are equally likely to be observed.

Interview-based occupancy modeling: is the use of systematic, carefully-conducted interviews with knowledgeable local residents to gather data on species presence. Local people selected as observers are associated with specific areas they have surveyed. Detection and non-detection of jaguars and prey is recorded for specific areas with multiple observers providing replicates in order to generate detection probabilities.

Metapopulation: coined as “a population of populations”, consists of a group of spatially separated populations of the same species where connectivity occurs and populations go extinct and are recolonized.

Northwestern Jaguar Recovery Unit (NRU) (U.S. Fish and Wildlife Service 2012, Sanderson and Fisher 2013): The 226,826-km² Northwestern Jaguar Recovery Unit (NRU) straddles the United States-Mexico Border with approximately 29,021 km² in the United States and 197,805 km² in Mexico.

Parabiologists: local people trained in scientific survey methodologies.

Peripheral areas (U.S. Fish and Wildlife Service 2012): are those areas included in general range maps that are inhospitable to jaguars, rarely having jaguar presence, and almost never supporting jaguars in recent times (last 100 years).

Criteria for peripheral areas:

1) Few verified historical or recent records of jaguars.

2) Habitat quality and quantity is marginal for supporting jaguar populations. Habitat may be in small patches and not well-connected to larger patches of high-quality habitat.

3) May sustain short-term survival of dispersing jaguars and temporary residents.

Precision: the amount of scatter, or repeatability, of the estimate when made many times. An estimate can be precise, yet, due to bias, off-target (compared to true population value), generating inaccurate estimates.

Prior distribution: is a key part of Bayesian statistical methods and represents the information about an uncertain parameter that is combined with the probability distribution of new data to yield the posterior distribution.

Recovery Units (National Marine Fisheries Service 2010): are subunits of a listed species that are geographically or otherwise identifiable and essential to the recovery of the species.

Secondary areas (U.S. Fish and Wildlife Service 2012): contain jaguar habitat with historical and/or recent records of jaguar presence with no recent record or very few records of reproduction. These areas are of particular interest when they occur between core areas and can be used as transit areas through which dispersing individuals can move, reach adjacent areas, and potentially breed. Jaguars may be at lower densities in secondary areas because of past control efforts, and, if future surveys document reproduction in a secondary area, the area could be considered for elevation to a core area.

Criteria for secondary areas:

1) Compared to core areas, secondary areas are generally smaller, likely contain fewer jaguars, maintain jaguars at lower densities, and contain more sporadic historical and current records. Evidence of occupancy may be weak or low because the area is not well surveyed, resulting in an unknown status of jaguars in these areas.

2) There is little or no evidence of recent (within 10 year) reproduction.

3) Habitat quality and quantity is lower compared to core areas.

Uniform prior distribution: in Bayesian statistical methods, a prior distribution where all intervals of the same length on the distribution's support are equally probable.

Literature Cited

National Marine Fisheries Service. 2010. Interim endangered and threatened species recovery planning guidance, version 1.3. Adopted by the U.S. Fish and Wildlife Service August 2010. Silver Spring, Maryland, USA.

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