

Protocol of Jaguar Survey and Monitoring Techniques and Methodologies

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TABLE OF CONTENTS

Table of Contents	i
Table of Tables	iv
Table of Figures	v
Executive Summary	1
Monitoring and Jaguar Conservation	4
Jaguars Across the Northwestern Recovery Unit	7
Jaguars in the Americas.....	7
Range Retraction on the Limits of Jaguar Range.....	7
Jaguar Conservation 1973 to Present	8
Jaguars in Mexico.....	9
Monitoring Jaguars in the NRU and Range Wide.....	10
Jaguar Status and Habitats in the NRU	10
Borderlands Secondary Area	11
Sonora Core Area	14
Sinaloa Secondary Area.....	17
Jalisco Core Area.....	18
Presence-Absence and Occupancy	22
Practical Considerations.....	22
Survey Protocol for Monitoring Jaguar Occupancy.....	24
Defining and Choosing Sample Units	25
Spatial Coverage of the Sample Unit	26
Sampling Duration.....	26
Setting Cameras.....	27
Data Recording.....	29
Data Analysis.....	31
Equipment and Costs.....	31
Logistical Challenges	32
Occupancy Modeling	33
Types of Occupancy Models	33
Pilot Data	35
Measuring Trends in Occupancy.....	35
Power Analysis	36

Occupancy Modeling for Prey Species	37
Sign-based Occupancy Sampling for Jaguars	39
Conclusion.....	40
Abundance and Density.....	42
Practical Considerations.....	44
Survey Protocol for Monitoring Jaguar Abundance and Density	47
Abundance/Density Estimation Field Techniques	47
Choosing Sampling Sites.....	47
Trap Distance, Camera Numbers, and Spatial Extent	48
Genetic Sampling for Abundance and Density	49
Sampling Duration.....	50
Setting and Checking Cameras.....	51
Surveying with Scat-Detection Dogs	52
Data Recording	52
Data Analysis.....	55
Equipment and Costs.....	56
Logistical Challenges	58
Capture-Recapture Modeling for Abundance and Density Estimation.....	58
Types of Abundance/Density Models	58
Pilot Data.....	61
Measuring Trends in Abundance/Density	61
Conclusion.....	62
Population Genetics	64
Jaguar Scat Collection.....	65
Opportunistic Searches	65
Scat Collection.....	65
Sampling Using Scat-Detection Dogs	67
Equipment and Costs.....	68
Laboratory Genetic Methods.....	68
DNA Isolation From Scat	68
Species Identification	69
Individual Identification	70
Costs	70
Analysis of Jaguar Scat Genetic Data	70

Species Identification	70
Individual Identification and Population Genetics	70
Demographic Parameters and Spatial Ecology.....	71
Dispersal and Long-Distance Movements	71
Demography	72
Survival and Recruitment.....	73
Home Range	76
Habitat Selection	78
Sampling Designs	79
Availability Data.....	80
Covariates	80
Data Analysis.....	81
Conclusion.....	85
Data Capture and Curation	87
Collection and export	87
Standardization and aggregation	88
Ingestion and Editing	88
Manual Editing	88
Automated Ingestion.....	88
Recommendations and Guidelines for Northwestern Recovery Unit and Beyond.....	90
Literature Cited	94
Appendix 1: Glossary	140
Appendix 2: April 2014 Workshop Participants.....	146
Appendix 3: Summary of the Application of Techniques	148
Appendix 4: Direct Jaguar and Puma Observations.....	156
Appendix 5: Collecting Data on Tracks and Scats	160
Appendix 6: Example Camera Setup Data Sheet	162
Appendix 7: Example Camera Checking Data Sheet.....	163
Appendix 8: Example Camera Test Card	164
Appendix 9: Example Photo-Captured Jaguars Data Sheet.....	165

TABLE OF TABLES

Table 1. The Northwestern Recovery Unit (NRU) by components..... 124

TABLE OF FIGURES

Figure 1. The 226,826 km ² Northwestern Jaguar Recovery Unit (NRU) straddles the United States-Mexico border with approximately 29,021 km ² in the United States and 197,805 km ² in Mexico.....	125
Figure 2. Known breeding populations in the Sonora Core Area occur in Sahuaripa-Huasabas and Alamos (yellow dots), and in the Jalisco Core Area occur in southern Sinaloa and Chamela-Cuixmala (green dots).	126
Figure 3. A grid of 452 500-km ² hexagons across the 226,826 km ² Northwestern Jaguar Recovery Unit (NRU).	127
Figure 4. A grid of 155 500-km ² hexagons across the 77,710 km ² Sonora Core Area in northern Mexico. Habitat suitability index at 1-km ² resolution, darker shades of green indicating higher suitability (Sanderson and Fisher 2013).....	128
Figure 5. Individual camera-trap locations within a 500-km ² hexagon in the 77,710 km ² Sonora Core Area in northern Mexico. Habitat suitability index at 1-km ² resolution, darker shades of green indicating higher suitability (Sanderson and Fisher 2013).....	129
Figure 6. Possible within-hexagon camera-trap setup maximizing spatial coverage.	130
Figure 7. Guido Ayala and Maria Vizcarra testing 2 camera traps set on opposite sides of a trail in Bolivia. Photo by Julie Maher.....	131
Figure 8. Camera trap sampling using paired cameras in the Upper Caura watershed, Guianan Shield Forests, Venezuela. Photo by Lucy Perera.	132
Figure 9. A standard template for the table in either csv or xls format is in the process of being specified, provisionally with the columns above.	133
Figure 10. Public interface to jaguar observation database (http://jaguardata.info/) developed by the Wildlife Conservation Society, showing controls that allow the user to filter by text, geographic location, year, event type, specificity of location and date, evidence type, and individual identity and sex.	134
Figure 11. User administration interface of the jaguar observation database (http://jaguardata.info/) developed by the Wildlife Conservation Society.....	135
Figure 12. Jaguar event listing of the jaguar observation database (http://jaguardata.info/) developed by the Wildlife Conservation Society.	136

Figure 13. Event editing interface of the jaguar observation database
(<http://jaguadata.info/>) developed by the Wildlife Conservation Society.....137

Figure 14. Editing a polygonal record area for association with non-point jaguar events of
the jaguar observation database (<http://jaguadata.info/>) developed by the
Wildlife Conservation Society.138

Figure 15. Zotero jaguar bibliography linked to the jaguar observation database
(<http://jaguadata.info/>) developed by the Wildlife Conservation Society.....139

EXECUTIVE SUMMARY

Jaguars (*Panthera onca* L.) have lived in the Americas for more than 2 million years, but thousands of years of range expansion were reversed in the last few hundred years, particularly on the margins of their range. Along the northern margin in the United States, 20th-century records with photographic evidence, skins, and skulls are available from New Mexico, Arizona, and Texas, while 21st-century observations are limited to southern Arizona and extreme southwestern New Mexico. Throughout this period, northwestern 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 the jaguar's range. The species is listed as Near-Threatened on the International Union for Conservation of Nature (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 (U.S. Fish and Wildlife Service 1997).

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 scale of the NRU, its gradients of jaguar abundance, and the threats to jaguar persistence in it, echo the situation across much of jaguar range. The USFWS contracted the Wildlife Conservation Society (WCS) to: 1) conduct a comprehensive literature review of jaguar survey and monitoring techniques and methodologies (Polisar et al. 2014); and 2) draft a jaguar survey and monitoring protocol for application in the NRU, with relevance for monitoring the species range wide. In this second half of the task, we present a survey and monitoring protocol for jaguars in the NRU and guidance for monitoring range wide.

In April 2014 WCS convened a group of fifteen jaguar and quantitative sampling scientists and agency personnel for a 4-day workshop at the Ladder Ranch in Caballo, New Mexico (see [Appendix 2](#)). Our goal was to develop a jaguar survey and monitoring protocol based on expert recommendations tailored to the habitats and social contexts of the NRU with application across the remainder of jaguar range. We considered the full range of possible sampling methods and modeling employed to document jaguar and other large carnivore population trends across time and space, before reaching consensus on a survey and monitoring protocol with a foundation in occupancy modeling centered on the NRU [Core Areas](#) using remote camera stations. We also discussed variations of that protocol and methods to evaluate abundance and density, population genetic characteristics, demographic parameters, components of jaguar spatial ecology, and mechanisms for data capture and curation. This multi-scale, expert-designed jaguar survey and monitoring protocol is a prescription for a package of complementary methods that can measure trends in a cost-effective way across the gradient of habitats and jaguar densities of core and

[secondary areas](#) in the NRU, as well as range wide. A summary of the application of recommended techniques is provided in [Appendix 3](#).

A critical question for jaguar conservation is are jaguar populations increasing, decreasing, or stable? The scales of jaguar range demands cost-effective repeatable metrics that can be applied across vast areas and multiple countries. At the core of our recommendations for monitoring large areas is occupancy to: 1) evaluate the current spatial distribution and estimate the proportions of areas occupied by jaguars; and 2) provide a low-cost baseline for evaluations of trends across time and space. Occupancy sampling provides indirect measures of jaguar abundance, and opportunities to test the influence of covariates of biological and management importance. Through occupancy the baseline of exactly where jaguars are and coarse indications of why they are there can be established.

Occupancy should be complemented by capture-recapture (CR) studies to estimate abundance in key areas and establish a baseline for numerical trends and demographic patterns. Constraining occupancy and CR surveys to 1 season can reduce variation due to jaguars making seasonal movements. Occupancy studies can provide an unbiased selection of study sites. In the case of camera-trap-based CR methods, we recommend numerous stations and ample spacing of stations. Multi-year scat surveys can also be used for genetic-based CR. For both methods of CR, we recommend very large sample areas. When human habitations occur near an area, preliminary work with local people to obtain consent and cooperation for the study helps develop communication and collaborations needed to effect jaguar conservation. We recommend spatially explicit capture-recapture models (SCR), but non-SCR models can be used to compare to previous studies, and to look at population trends. We provide guidance on study design, data collection during study, incidental data collection, data processing, storage, and analyses for all the above.

Camera-trap-based CR can provide a foundation for long-term studies of numerical trends and demographic patterns, but the information they provide on movements is limited. Dispersal data is best obtained through GPS satellite telemetry. Population genetics can also provide data about movements and relatedness.

Habitat selection can be analyzed using occupancy covariates, CR covariates, and detailed location data obtained through telemetry data. Although environmental correlates may be coarse-scale data drawn from remote sensing, when fine-grained data are obtained from telemetry, they should be complemented by equally fine-grained real-time data about the distribution of resources, threats, and environmental parameters in the study area. We provide recommendations on the estimation of study animal home ranges, and suggestions on how to assess resources within them.

Demographic patterns can be estimated using camera traps or telemetry, but in both cases require long-term, data-rich studies. Occupancy can serve as a metric of jaguar status and recovery in the

NRU, on a 5-year jaguar generation level or on a 15-year level (3 jaguar generations). Occupancy also has applications on a larger scale, for assessments of the status of jaguars, either range wide, or at eco-regional levels. Studies on numerical trends, demography, and dispersal are an important component of regional jaguar study plans. Ultimately, the conservation of jaguars is effected by counteracting indirect and direct threats. Large-scale monitoring of jaguars will inform us on how well we are doing.

MONITORING AND JAGUAR CONSERVATION

Monitoring threatened and endangered species is needed to inform management actions. One can monitor status of a species, pressures (threats) to that species, and responses of that species to management interventions (Jones et al. 2013). One also can monitor social factors such as the efficacy of outreach intended to change the public's attitudes and practices for those who coexist with threatened and endangered species. Population parameters (spatial distribution, density, population size, survival, and recruitment) reflect responses to management interventions. Monitoring of indirect threats, while not emphasized here, is also recommended for a comprehensive species conservation and recovery program.

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.” Surveys are exploratory, but done well they provide the baseline for repeated measures.

Monitoring can be viewed as the repetition of survey methods to make inferences about trends in abundance, and/or distribution, and the relative importance of management or ecological attributes. This can provide measures of recruitment, survival, dispersal, and local colonization and extinction. Every hypothesis requires a research design that will address the question it poses, and an analytical framework to draw inferences from the data at an adequate level of accuracy. 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) needs to be predefined. The cost of the monitoring needs to be considered in the context of the value of the improved decision making it enables (Jones et al. 2013).

Which foci of monitoring should be deployed depends in part on a gradient of a species status, ranging from secure populations to dispersing animals in peripheral areas. Jaguars (*Panthera onca* L.) 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*). Because the jaguar still occurs in over 50% of its historical range, range-wide monitoring implies an immense scale that includes Jaguar Conservation Units (JCU; Sanderson et al. 2002), which function as sources, and a matrix of secondary and [peripheral areas](#), which may connect to other JCUs and be used as [corridors](#) by dispersing individuals.

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). Due to habitat conditions and local eradication, jaguars in the NRU may currently be at low densities compared to some other parts of the jaguar's range, but the configuration of core areas, secondary areas, and peripheral areas in the NRU mirrors the challenges of monitoring across gradients range wide.

Monitoring habitat is an important complement to population-focused monitoring. The availability of habitat suggests potential for occupancy and potential for recovery, but habitat status alone does not translate directly to jaguar status. Prey abundance and biomass may be more reliable indicators of potential high quality habitat for jaguars. Even when correlations can be established between habitat type and jaguar presence or abundance, population focused sampling is necessary.

Because monitoring requires a baseline, initial surveys should be accurate, yet sufficiently cost-effective to allow long-term repeated measures. Where jaguar densities are extremely low, spatial presence-absence approaches will cover large areas with less cost. In source areas where jaguars are secure, intensive capture-recapture and telemetry studies can assess abundance, demographics, and dispersal.

The current net measure of the jaguar's status across its range (stable, decreasing, or increasing) has yet to be established. Significant parts of the jaguar's range are still experiencing escalating land conversion, prey depletion, and direct killing of jaguars. In other areas, the jaguar's status is relatively constant, and in some areas, recovery is taking place. Thus far we have lacked adequate repeated measures from a sufficient subset of significant JCUs to comment authoritatively on global trends. Establishing this framework for repeated measures and trend assessment is a step towards range-wide, integrated assessments and monitoring.

The U.S. Fish and Wildlife Service (USFWS) contracted the Wildlife Conservation Society (WCS) to: 1) conduct a comprehensive literature review of jaguar survey and monitoring techniques and methodologies (Polisar et al. 2014); 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 second task, we present a survey and monitoring protocol for jaguars. The protocol is designed for professionals seeking appropriate techniques and methodologies to estimate jaguar presence, occupancy, abundance, and density. The protocol balances the effectiveness of the techniques and methodologies, and accuracy and quality of the results, with the cost of conducting the protocol. The protocol includes a thorough overview of each technique with illustrations and descriptions of data storage and analysis techniques.

The goal of this protocol is to provide recommendations for jaguar survey and monitoring techniques and methodologies for the NRU, with relevance for monitoring the species range wide. We provide a suite of survey and monitoring methods requiring a range of survey

intensities, resource requirements, and degrees of [precision](#). We begin with a review of jaguar records and the physical, ecological, and management characteristics of the NRU. We describe ecological and logistical realities to provide the necessary on-the-ground context for the recommended survey and monitoring techniques. We then discuss survey and analytical methods to determine jaguar presence-absence and occupancy. These survey methods are centered on the Sonora and Jalisco Core Areas using remote camera stations. We then discuss methods used to adapt presence-absence and occupancy surveys to quantify estimates of jaguar abundance and density using spatially explicit capture-recapture techniques. We continue with a discussion of the use of scat-detection dogs (*Canis lupus familiaris*) to survey for scats in areas of high probabilities of jaguar occupancy. Genetic material is necessary to evaluate metrics of genetic distance and inbreeding coefficients. We then discuss the use of biotelemetry in areas with high jaguar densities to estimate jaguar survival, reproduction, dispersal, home ranges, and habitat selection. We conclude with a discussion on data capture and curation, and monitoring recommendations for the NRU and beyond.

Where there are multiple possibilities, we review each, discussing strengths and weaknesses. Likewise, if there is a very effective but costly approach, we offer a lower cost option and describe the differences. The recommendations we present will be relevant for source areas, their margins, and the corridors between them.

JAGUARS ACROSS THE NORTHWESTERN RECOVERY UNIT

Jaguars in the Americas

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 (extant) felids in the New World, with adults typically having a head and body length of 1-2 m and body mass from 36-158 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 such as cattle and sheep (e.g., Rosas-Rosas et al. 2010). They compete successfully with pumas (*Puma concolor* L.), but 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 occur in mountains up to 2,000 m and utilize beaches (Troeng 2001). It is not well understood what limits their range beyond the need for cover, food, 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 of the other roaring cats from the *Panthera* genus and immigrated across the Beringia land bridge, expanding across North America and into South America. In the United States, remains of jaguars from the Pleistocene have been found in 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).

Range Retraction on the Limits of Jaguar Range

Thousands of years of range expansion have been reversed in the last few hundred years, particularly on the margins of the range. We focus here on the losses in the northern part of the jaguar's range, in particular. 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, 19th 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, Merriam 1919, Strong 1926, Nowak 1973, Brown and

López-González 2001). A much smaller number of difficult-to-interpret, but intriguing, observations are found from the 18th century from points much farther east than what is now commonly considered jaguar range in the United States (e.g., Brickell 1737, Ford 1904). 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 (U.S. Fish and Wildlife Service 2014).

Throughout the last 100 years, Mexico has remained a harbor for jaguar populations at the northern end of the range, including in wilder parts of Sonora (Burt 1938, Leopold 1959, Landis 1967, Carmony and Brown 1991, Brown and López-González 2001, Grigione et al. 2009). Numerous summary reviews of the observational history of jaguars in the U.S.-Mexico Borderlands 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 the NRU in a searchable, relational database (Sanderson and Fisher 2011, 2013). The loss of jaguar range in the United States and extreme northern Mexico mirrors losses at the southern end of the range and in other places where human land use has driven out jaguar prey (Swank and Teer 1989, Sanderson et al. 2002, Zeller 2007).

Jaguar Conservation 1973 to Present

As a result of decreases in jaguar distribution, habitat, and prey base, jaguars 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, anthropogenic activities reducing connectivity (e.g., border infrastructure), limitations in enforcing regulatory mechanisms across national boundaries, and climate change (U.S. Fish and Wildlife Service 2012). Although the fur trade stopped in the 1970s, direct killing has remained a significant source of mortality, and population declines occur, especially in areas where poorly-managed ranching overlaps occupied jaguar habitat, and individuals learn to take livestock. Often in these situations, both targeted control and indiscriminant killing of jaguars ensues.

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 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 150 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 (Sanderson et al. 2002). It is connected to pockets of potential habitat north of the border by dry, desert conditions and steep mountain ranges. Anthropogenic activity (e.g., urbanization, roads, land development, and border fence construction to deter illegal human immigration and terrorism threats from entering into the United States) may negatively impact connectivity for wildlife (Atwood et al. 2011), including jaguars (U.S. Fish and Wildlife Service 2012). Yet jaguars have been moving through from Mexico into the United States (McCain and Childs 2008).

Jaguars in Mexico

In 2005, the Instituto de Ecología de la Universidad Nacional Autónoma de México (UNAM), with support of the Comisión Nacional de Áreas Naturales Protegidas (CONANP), 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 were 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). Annual national symposia were held to develop an action plan to determine conservation strategies for the jaguar in Mexico, select a standard methodology to use for the National Jaguar Census (CENJAGUAR; 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). The National Jaguar Census 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, Medellín 2009, Zarza et al. 2010, Caso et al. 2011, Núñez-Pérez 2011, U.S. Fish and Wildlife Service 2012, Panthera 2013). Currently the Mexico government is supporting efforts to evaluate jaguar populations in the NRU through the Programa de Conservación de Especies en Riesgo (PROCER; Program for the Conservation of Species At Risk) of the Dirección de Especies Prioritarias para la Conservación (Priority Species Division) of CONANP.

Monitoring Jaguars in the NRU and Range Wide

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 core areas (Jalisco 54,949 km² and Sonora 77,710 km²), as compared to the secondary areas (Sinaloa 31,191 km², Borderlands – Mexico 33,955 km² and United States 29,021 km²), based on cost-benefit ratios.

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), Rosas-Rosas and Bender (2012), Núñez (2013), Núñez y Vazquez (2013), and Culver et al. (2014). Despite these recent efforts, jaguar presence, occupancy, abundance, density, population trends, and demographic parameters are not well known in the NRU (U.S. Fish and Wildlife Service 2012). 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 combination of core areas and the connections among them provides an exciting opportunity to design effective large-scale monitoring

Monitoring jaguar populations across the vast NRU and in similar strongholds and secondary areas throughout jaguar range will provide for the detection of growth or retraction in space occupied, estimation of jaguar numbers, and evaluation of population trends. Based on the logistical challenges and varied terrain and habitat types, a mix of the methods prescribed in this document will be necessary. A cost-effective mix of methods should begin with presence and presence-absence spatial approaches. Abundance studies, which monitor numbers of jaguars, are merited for areas where jaguars are more abundant (core areas).

Jaguar Status and Habitats in the NRU

Jaguar presence in the NRU has recently been documented from the Arizona and New Mexico borders south through the Sierra Madre Occidental to Colima, encompassing a variety of habitat types from pine-oak forest to semi-tropical thorn-scrub to tropical deciduous forest (López-González and Brown 2002, Valdez et al. 2002, Núñez-Pérez 2007, 2011, McCain and Childs 2008, Núñez 2012). The threats that jaguars face range wide (habitat modification and fragmentation, reduction of prey populations, and predator control practices) also prevail in northern Mexico (Valdez 1999, López-González and Brown 2002, Rosas-Rosas et al. 2008), where the main threats to jaguar conservation are illegal predator control, illegal hunting of prey species, and habitat degradation (López-González and Brown 2002, Rosas-Rosas and Lopez-Soto 2002, Valdez et al. 2002, Rosas-Rosas et al. 2008, Rosas-Rosas and Valdez 2010, Rosas-

Rosas and Bender 2012). The current lack of adequate law enforcement, inadequate community and landowner conservation programs, and unsustainable natural resource extraction play a role in habitat modification and fragmentation, reduction of prey populations, and predator control practices. There is an urgent need to address both indirect and direct threats to maintain existing jaguar populations and achieve recovery in the NRU.

Borderlands Secondary Area

The 62,976 km² Borderlands Secondary Area includes 29,597 km² of [suitable habitat](#) and 431 km² of [core habitat](#) in portions of southeastern Arizona, southwestern New Mexico, northwestern Sonora, and northeastern Chihuahua (Kim Fisher, Wildlife Conservation Society, personal communication; [Table 1](#); [Figure 1](#)). The area is a region of north-south trending, forested and shrub covered mountain ranges surrounded by lower desert valleys and plains, straddling the current United States-Mexico border (Brown 1983, Brown and López-González 2000, 2001). Habitat conditions suitable for jaguars include vegetative cover, access to water, and freedom from persecution (Hatten et al. 2005) and primarily found in the area in the topographically complex mountain areas frequently referred to as “Sky Islands.” Madrean evergreen woodland, a mixture of oak and pine forest, is an important habitat, as are higher elevation montane conifer forests and piñon-juniper woodlands (Rabinowitz 1999, Brown and López-González 2001, Hatten et al. 2005). These habitats are uncommon across the jaguars entire range (Sanderson et al. 2002), making this area of potentially global significance for jaguar conservation. However, the area is compromised by its limited extent of suitable habitat as currently defined, its relatively high human footprint (compared with some areas in other subsections of the NRU), and the presence of the border security fence, potentially separating habitat areas in the United States and Mexico. The desert valleys, which comprise most of the areal extent of this secondary area, are thought to provide little habitat value, although repeat captures in camera track studies indicate that at times jaguars do cross these areas (McCain and Childs 2008).

Potential prey species in the Borderland Secondary Area include collared peccary (*Tayassu tajacu*), white tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), coatis (*Nasua nasua*), skunk (*Mephitis* spp., *Spilogale gracilis*), raccoon (*Procyon lotor*), jack rabbit (*Lepus* spp.), domestic livestock, and horses (Brown and López-González 2001, Hatten et al. 2005).

Jaguars appear to take advantage of north-south trending mountain ranges to facilitate movements in the Borderlands Secondary Areas. The US-Mexico Barrier crosses these mountain ranges on an east-west axis in order to inhibit illegal human movements across the border. Special management considerations or protections should address threats posed by increased human disturbances into remote locations through construction of impermeable fences and widening or construction of associated infrastructure. Jaguars have been heavily hunted within the United States in the past and are currently hunted in parts of Mexico (Brown and López-González 2001). A jaguar was killed illegally in 1986 in the Dos Cabezas Mountains of Arizona,

for example. Given the small population in this part of the NRU, any hunting pressure is a threat. Hunting of jaguar prey may also represent a threat, particularly if it leads to jaguars utilizing domestic livestock rather than native prey. Human-wildlife conflict over depredation of domestic animals, whether caused by jaguars or sympatric predators (like pumas) increases the threat to jaguars in other parts of the range (Zimmerman et al. 2005, Michalski et al. 2006). Finally, the habitat is so limited in the Borderlands Secondary Area it is unclear whether it can sustain a viable population of jaguars as currently delimited (Miller 2013). Habitat limitations are the result of the natural topography of the area, the distribution of native vegetation, and the development of human settlements and infrastructure in valley bottoms and foothills. The lack of habitat for a wide-ranging carnivore can be considered a threat in this part of the range (Eric Sanderson, Wildlife Conservation Society, personal communication).

Jaguars have long been documented in the Borderlands Secondary Area (Brown 1983, Brown and López-González 2000, 2001). Native American groups from this area have specific names for jaguars (Daggett and Henning 1974, Brown and López-González 2001, Pavlik 2003), some of which may predate European settlement during the 16th and 17th century. The first scientific survey in the area was associated with the survey of rail routes after the Mexican-American War by Baird (1857), who observed a jaguar in the Santa Cruz Valley. American settlers and ranchers in the Arizona territory in the late 19th and early 20th century left numerous accounts of jaguar hunts, summarized by later scientists from press accounts, interviews, and historical records (Schufeldt 1929, Bailey 1931, Cahalane 1939, Halloran 1946, Hock 1955, Brown 1983, Brown and López-González 2001, Grigione et al. 2007, Sanderson and Fisher 2011); similar accounts are also known from adjacent parts of Mexico (Burt 1938, Leopold 1959, Brown and López-González 2001).

In the U.S. portion of the Borderlands Secondary Area, government hunters and trappers working on behalf the United States government killed jaguars in this area in 1917, 1919, 1924, 1926, 1932-1933, and 1964 (Brown and López-González 2001). Jaguars were occasionally taken through the 1950s-1970s, although some of these animals may have been brought to the area as part of “canned hunts” (Brown and López-González 2001, Grigione et al. 2007, Brown and Thompson 2010, Sanderson and Fisher 2011). A jaguar was killed in the Dos Cabezas Mountains of Arizona in 1986 (U.S. Fish and Wildlife Service 1994). Two jaguars were photographed in 1996, 1 by Warner Glenn in Hog Canyon, near the Arizona / New Mexico border (Glenn 1996), and the other by Jack and Anna Childs in the Baboquivari Mountains in extreme southern Arizona (Childs and Childs 2008). McCain and Childs (2008) were later able to identify 2 different jaguars through camera trapping surveys in 2003, Macho A and Macho B. Macho A disappeared shortly thereafter, but Macho B was photographed repeatedly in the Baboquivari and Atascoca Mountains through March 2009. As of 2011, at least 1 jaguar is known to occur in the United States (Ames and Wasu 2011) in the Borderlands Secondary Unit.

In the Mexico portion of the Borderlands Secondary Area, since 2009, 2 jaguars have been documented at Rancho El Aribabi, Sonora, about 48 km southeast of Nogales, and 1 jaguar has

been documented in the Sierra Los Ajos within the Reserva Forestal Nacional y Refugio de Fauna Silvestre Ajos-Bavispe, about 48 km south of the U.S. border near Naco, Mexico (USFWS 2012). This individual was photographed in 2009 and 2013 in the area. In August 2012, in Papigochic, Sonora about 60 km south of the U.S. border, near of Cananea a jaguar track was seen in a private cattle ranch. In 2013, 1 jaguar male was photographed inside Janos Biosphere Reserve in the limits between Chihuahua and Sonora about 70 km south of the U.S./Mexico border (Carlos López González, University of Querétaro, personal communication).

There are numerous protected areas on the U.S. side of the border managed by a variety of different federal, state, and tribal entities which collectively protect 3,674 km² (Conservation Biology Institute 2012, CONAP). There are also a number of privately managed conservation areas. On the Mexico side of the border there is only one protected area, the Janos Biosphere Reserve, which only intersects the Borderlands Secondary Area slightly on the eastern edge.

In March 2014, the USFWS designated approximately 3,092 km² in Pima, Santa Cruz, and Cochise Counties, Arizona, and Hidalgo County, New Mexico, as [critical habitat](#) for the jaguar (U.S. Fish and Wildlife Service 2014). Critical habitat is designated in 6 units organized to encapsulate mountain ranges used by jaguars at least once since 1962.

The Borderlands Jaguar Detection Project led by Jack Childs monitored jaguars in southern Arizona from 2002-2010. McCain and Childs (2008), following 2 sightings of jaguars in 1996, established a remote camera survey using approximately 40 cameras extending from the crest of the Baboquivari Mountains east to the San Rafael Valley and approximately 80 km north of the U.S.-Mexico border. The study area encompassed biotic communities of Madrean evergreen woodland and semidesert scrub grassland. McCain and Childs (2008) documented 2 adult male and possibly a third unidentified jaguar with 69 photographs taken by remote cameras and 28 sets of tracks.

A 3-year project for detection and monitoring of jaguars and other wildlife biodiversity, in southern Arizona and southern New Mexico, was started in October 2011 by a team of biologists at the University of Arizona led by Melanie Culver. Researchers are using approximately 280 remote cameras and noninvasive genetic methods across 16 mountain ranges. As of October 2014 this effort has documented one male jaguar. The project will conclude in June 2015. Mexican investigators Jesus Moreno and Rodrigo Medellin have been monitoring wildlife, including jaguars, in an UMA in the Aros-Bavispe area of Sonora, Mexico from 2000 until present.

Led by Dianna Hadley, the Northern Jaguar Project together with Naturalia has also been conducting remote camera surveys, in the Aros-Bavispe area, but on privately owned lands. The Sky Island Alliance has been monitoring jaguars at the Rancho El Aribabi in Sonora Mexico, using remote cameras and has detected 2 jaguars to date.

Sonora Core Area

The 77,710 km² Sonora Core Area includes 67,889 km² of suitable habitat and 28,294 km² of core habitat in portions of southwestern Chihuahua, northeastern Sinaloa, and Sonora (Kim Fisher, Wildlife Conservation Society, personal communication; [Table 1](#); [Figure 1](#)). The northernmost known breeding population of jaguars in North America is located in northeastern Sonora, Mexico (López-González and Brown 2002, Valdez et al. 2002). The area is located in the northern portion of the Sierra Madre Occidental, which is the largest mountain range in northwestern Mexico. The Sierra Madre Occidental encompasses a variety of habitats including pine, oak-pine, semitropical deciduous forests, oak woodlands, and semitropical thorn-scrub (Brown 1982). The jaguar population in Sonora represents the potential dispersal center for movements farther north, and is critical to any naturally occurring re-establishment of a jaguar population in the southwestern United States (McCain and Childs 2008).

There are diverse potential jaguar prey species in Sonora, but the most common ungulates present are white-tailed deer and collared peccary. Carnivores present other than jaguars and puma are coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), bobcat (*Lynx rufus*), ocelot (*Leopardus pardalis*), river otter (*Lontra longicaudis*), badger (*Taxidea taxus*), skunks (*Mephitis* spp., *Spilogale* sp., *Conepatus* sp.), white-nosed coati (coati), and ring-tailed cat (*Bassariscus astutus*), raccoon, and margay (*Leopardus wiedii*) (Leopold 1959, Hall 1981). The primary prey for jaguars in this area are Coues white-tailed deer (*Odocoileus virginianus couesi*) and collared peccary, and, to a lesser extent, coati, opossum (*Didelphis virginiana*), and lagomorphs (Rosas-Rosas et al. 2008). Cattle are the predominant domestic mammals, and also constitute a prey item in northern Sonora.

With cattle ranching being one of the most important economic activity and culture in Sonora, cattle losses due to predation by jaguars and pumas are considered a major threat and nuisance, regardless of their economic impact. Hence, human-jaguar conflicts constitute one of the main factors limiting jaguar populations, numerically and spatially, in the northernmost part of the species' range, and may represent the primary limitation to incremental jaguar recovery farther north. That said, fairly recent innovative efforts have been made to motivate ranchers to tolerate jaguars, including the work conducted Rosas-Rosas and Valdez (2010) and the NJR Rosas-Rosas and Valdez (2010) worked with ranchers to develop a jaguar conservation program based on white-tailed deer trophy hunts to compensate cattle losses from predation by jaguars.

In Sonora, most jaguar records are from semi-tropical thorn-scrub, oak and oak-pine forest, and tropical deciduous forest (Martínez-Mendoza 2000, López-González and Brown 2002, Rosas-Rosas 2006). The majority of records are from cattle ranches, private refuges, and [Áreas Naturales Protegidas \(ANPs\)](#). There are a number of areas that were established for the protection of jaguars or that contribute to jaguar conservation in Sonora, including 2 in northeastern Sonora, the Northern Jaguar Reserve (NJR) and the [Unidad de Manejo para la Conservación de Vida Silvestre \(UMA\)](#) of the Asociación para la Conservación del Jaguar en la

Sierra Alta de Sonora (Asociación para la Conservación del Jaguar en la Sierra Alta de Sonora UMA), and 1 in southern Sonora, the [Área de Protección de Flora y Fauna Silvestre \(APFF\)](#) Sierra de Álamos-Río Cuchujaqui (APFF Álamos-Río Cuchujaqui).

Northern Sonora

In northeastern Sonora, 2 areas that were established to benefit jaguars include the Asociación Alianza para la Conservación del Jaguar en la Sierra Alta de Sonora UMA and the NJR. While there are several UMAs in Sonora that benefit the jaguar and its habitat, the Alianza para la Conservación del Jaguar en la Sierra Alta de Sonora UMA, established in 2003 and located 210 km south of the United States-Mexico border in northeastern Sonora, is the only one formally created to benefit jaguars. Eleven properties of the 8 participating landowners encompass 400 km². The purpose of this unit is to compensate cattle ranchers for livestock depredation by predators and to generate alternative income for cattle ranchers. Coues white-tailed deer trophy hunting and associated ecotourism are the main economic activities. Scientific advisory of the UMA Sonora is executed by the Instituto de Ecología of the Universidad Autónoma de México in Mexico City.

The NJR began in 2003 with the purchase of 1 ranch in northeastern Sonora, about 220 km south of the United States-Mexico border, and, over time, has grown to a total of approximately 200 km² through the purchase of additional property. The reserve was established to safeguard and restore wildlife habitat (particularly for jaguars), to support wildlife research and educational programs, and to reduce conflicts between carnivores and humans. This private protected area is managed jointly by Naturalia (a Mexican conservation organization) and the Northern Jaguar Project (NJP).

Jaguar research projects have been conducted in northern Sonora within both the NJR and Asociación para la Conservación del Jaguar en la Sierra Alta de Sonora UMA (referred to as Sahuaripa-Huasabas in Figure 2), as well as some areas adjacent to the NJR (López-González and Brown 2002, Rosas-Rosas and Valdez 2010, Rosas-Rosas et al. 2010, Gutiérrez-González et al. 2012, Rosas-Rosas and Bender 2012). Gutiérrez-González et al. (2012) conducted a capture-recapture study to estimate jaguar density in the NJR and adjoining cattle ranches that had agreed not to hunt wildlife. The vegetation in this 330 km² area was a mosaic of dry thorn-scrub, semi-deciduous forest, riparian vegetation including palms and oaks, and natural grasslands. Mean annual precipitation was less than 400 mm annually, distributed throughout the year but with winter rains accounting for 18%. Mean annual temperatures ranged from 16-30° C with extremes between -7 and 43° C. Camera-trap sampling across 16 months, with a variable number of camera traps (25-111) and a total of 7,718 trap-nights, yielded 63 jaguar photo-captures of 10 individuals. Using the Jolly-Seber open population model, the authors estimated jaguar density at 1.05/100 km² in this area (Gutiérrez-González et al. 2012).

Rosas-Rosas and Bender (2012) combined camera-trap and track surveys to assess jaguar and puma status in a 400 km² study area in the Alianza para la Conservación del Jaguar en la Sierra Alta de Sonora UMA in the foothills of the Northern Sierra Madre Occidental in an area of rocky and rugged topography. The main vegetative community in this area was a semi-tropical thornscrub. This area contained intermittent and perennial streams, and, depending on elevation (which ranged from 500-1,500 m above sea level), an annual precipitation of 400-1,000 mm. The area experiences a dry season (October-June) and a wet season (July-September), the latter of which is characterized by short-duration, high intensity downpours. , Camera traps were deployed in 26 stations for 60 days. Intensive track surveys recorded 208 jaguar tracks, identifying 12 individuals through idiosyncratic features of their forefeet. Transients were also identified. From 159 puma tracks, 14 different pumas were identified. Discriminant functions based on track measurements complemented visual identifications and confirmed an 87.4, 84.9, 73.7, and 82.3% correct classification of male and female jaguars and pumas, respectively. Based on information collected during 1,560 trap-nights augmented by track observations, the authors estimated 4 jaguars/360 km², or approximately 1 jaguar/100 km² in this area (Rosas-Rosas and Bender 2012).

Additionally, [Primero Conservation](#) and the Asociación para la Conservación en la Sierra Alta de Sonora operated camera traps continuously on several ranchlands within the Asociación para la Conservación del Jaguar en la Sierra Alta de Sonora UMA in mountainous, dry-tropical thornscrubs ranging between 440 m and 1,230 m above sea level between April 2009 and September 2011. Cameras were checked opportunistically during ranch operations (Cassaigne 2014). Camera traps in 38 stations sampled an area of approximately 408 km² (it is not clear if the area was formed by the mean or maximum outer band of the camera trap stations or if that dimension was increased by an estimated buffer) for 8,408 trap-days over 2.5 years (Moreno et al. 2013).

For each camera location in this study, independent pictures of a single species were defined to be those pictures taken more than 1 hour apart. Sequential pictures of the same species at the same location were considered redundant. Eleven jaguars and 9 ocelots were individually identified, and densities of each species were estimated with SPACECAP (2.7 jaguars/100 km², ocelots 2.2/100 km²). Moreno et al. (2013) documented species occurrence rates (species recorded at a station) at the 38 stations of: 34 puma 33 white-tailed deer, 31 cows, 30 coati, 23 bobcat, 19 desert cottontail (*Sylvilagus audubonii*), 12 collared peccary, and 6 raccoon which provides a useful sketch of the spatial distribution of these species and coverage of the study area. Relative abundances, based on percent of all the independent photos, were puma 3.32, deer 13.25, cows 35.43, coati 1.92, bobcat 2.20, jaguar 0.96, desert cottontail 7.59, collared peccary 0.18, and raccoon 0.20. The contrasts seen between very low relative abundance of peccaries (a natural prey item throughout much of jaguar range), and the high relative abundance of cattle (something we really hope to not see in jaguar diets), points to a potential source of human-jaguar conflicts and a conservation issue that needs to be rectified.

Collared peccary frequencies in this study area were notably low. With the exception of white-tailed deer, the biomass of natural jaguar prey was low, while cattle biomass was high and appeared to have been evenly distributed throughout the study area. The survey results suggested that the resident jaguars were subsidized by livestock which tends to increase jaguar mortality due to retaliatory killing. Primero Conservation initiated analyses of exposure to canine distemper virus (CDV) in peccaries, feral dogs, coyotes (*Canis latrans*), puma, and jaguar (Cassaigne 2014). To reduce the risk of retaliatory killing due to jaguars depredating livestock, Primero Conservation responded to the low peccary populations by translocating peccaries vaccinated against canine distemper virus from Arizona after governmental inspection and permitting, with soft releases planned for 2013. The preliminary assessments of jaguar prey indicated depressed collared peccary populations, with the above efforts intended to improve peccary status, hence potentially reducing human-jaguar conflicts.

Southern Sonora

Farther south in Sonora in the municipality of Alamos (Figure 2), the APFF Álamos-Río Cuchujaqui is a 928-km² area that was established in 1996 to regulate the sustainable use of water, soil, and wildlife. Ranging between 300 and 1,720 m above sea level, the reserve includes tropical deciduous forest, pine-oak forests, Sinaloan thorn-scrub, and riparian vegetation, and is considered a [Biosphere Reserve](#) by the United Nations Educational, Scientific, and Cultural Organization, as well as the state of Sonora. Additionally, the Arroyo Verde ecosystem within the Biosphere Reserve is a [Ramsar Site](#) based on 3 streams included in the reserve and its notably high biodiversity due to a mix of northern and tropical biota. Land ownership within this reserve is primarily [ejido](#) (communally-owned lands) and private, although a small portion is federal. This area is recognized as an ANP by CONANP, and is managed as such.

Gutiérrez-González (2013) deployed 25 camera-traps for 3 months during a recent jaguar survey in the APFF Álamos-Río Cuchujaqui. Six individual jaguars were identified from the estimated effective sampling area of 330km². Jaguar density was estimated to be 2.13 ± 1.06 individuals/100 km² using the capture-recapture models in Program MARK.

Sinaloa Secondary Area

The 31,191 km² Sinaloa Secondary Area includes 28,753 km² of suitable habitat and 18,847 km² of core habitat across approximately one third of eastern Sinaloa (Kim Fisher, Wildlife Conservation Society, personal communication; [Table 1](#); [Figure 1](#)). Tropical deciduous forest and higher elevation oak-pine forests cover 40 and 15% of the state, respectively (Navarro-Serment et al. 2005). The coastal plain (35% of Sinaloa) is being transformed for agriculture, aquaculture, and human settlement, leaving few adequate habitat patches for jaguars. Although there are areas that have been identified as priorities for conservation by CONABIO, none of them currently are formally protected.

Potential jaguar prey in the area include armadillo, coatimundi, collared peccary, white-tailed deer, and introduced European wild boar or feral hog (*Sus scrofa*).

The Sinaloa Secondary Area, which is thought to support a smaller population that may suffer the ill effects of inbreeding depression, demonstrates less vigorous growth potential, especially when dispersal amongst nearest neighbors is rare (Miller 2013). Poaching and killing of jaguars by ranchers protecting livestock can significantly increase mortality in Core Areas, which could in turn reduce the number of dispersing individuals received by smaller population units like those in the Borderlands Secondary Area (Navarro-Serment et al. 2005, Miller 2013).

Interview-based surveys by Navarro-Serment et al. (2005) found most jaguars occurred in the tropical deciduous forest that still covers 40% of Sinaloa. Only 2 records came from the higher-elevation oak-pine forests that cover 14.7% of the state. Only 1 record was obtained in riparian vegetation. Prey densities (armadillo, coatimundi, white-tailed deer, and collared peccary) appeared to be high in the mountains of Sinaloa, where extensive areas of tropical deciduous forest remain. The records in 2005 suggested that a jaguar population still existed in Sinaloa, but the information gathered through interviews needs to be confirmed through field studies.

Camargo-Carrillo carried out an interview survey throughout the State of Sinaloa that documented a total of 133 jaguar records, most coming from the southern portion of the state (i.e., the Jalisco Core Area; Carlos López-González, University of Querétaro, personal communication); however, few records were obtained from within the Sinaloa Secondary Area. Additionally, Camargo-Carrillo identified an area of occupied jaguar habitat south of the APFF Álamos-Río Cuchujaqui as vulnerable to human development.

Gutiérrez-González et al. (2013) deployed 25 remote cameras were for 3 months, yielding 1 individual jaguar photographed in the area known as El Fuerte in the Sinaloa Secondary Area.

Jalisco Core Area

The 59,949 km² Jalisco Core Area includes 44,404 km² of suitable habitat and 26,315 km² of core habitat in southern Sinaloa, Nayarit, and Jalisco (Kim Fisher, Wildlife Conservation Society, personal communication; [Table 1](#); [Figure 1](#)). Along the northern coast in Cabo Corrientes and Puerto Vallarta municipalities, an area of high topographic relief (0-1,800 m above sea level), jaguars use tropical dry and semi-deciduous forest.

In protected areas of Jalisco and Nayarit, white-tailed deer, collared peccary, nine-banded armadillo, raccoon, and coati area are the main jaguar prey (Núñez et al. 2002). In the wetlands, raccoons are important prey (Rodrigo Núñez, Proyecto Jaguar, personal communication). However, in areas with a high presence of livestock and lack of natural prey, livestock comprise a food item (Rodrigo Núñez, Proyecto Jaguar, personal communication).

Tropical dry and semi-deciduous forests have been reduced and fragmented due to pressure from agriculture and cattle ranching, and infrastructure development (roads and tourism development associated with the world class beach resorts of western Mexico) may bring increasing fragmentation.

Most jaguar records in the Jalisco Core Area come from hilly terrain covered by low-growing, tropical dry and sub-deciduous forest, with a smaller proportion of locations from oak-pine forest. Núñez (2007) described 6 priority jaguar conservation sub-units in the Jalisco Core Area: 3 in Jalisco and 3 in Nayarit. Research within the region has been focused in 4 sites: 1 in Nayarit and 3 in Jalisco. The most intensive surveys have been conducted in 3 federally-recognized Biosphere Reserves: la Reserva de la Biosfera Chamela-Cuixmala (RBCC), la Reserva de la Biosfera Sierra de Manantlán (RBSM), and la Reserva de la Biosfera Marismas Nacionales Nayarit (RBMNN). The only long-term study has been conducted in the RBCC. Two additional areas where jaguar surveys are ongoing are volunteer-protected UMAs.

Jalisco

The 130-km² RBCC in Jalisco (Núñez et al. 2000, Núñez-Pérez 2006, 2011) is a private reserve also recognized as an ANP. It was established in 1993 and could be considered the core of the Jalisco Core Area. The reserve extends east from the Pacific Ocean and reaches elevations of about 700 m above sea level. The terrain is rugged with arroyos separating prominent hills. Because the average of 700 mm of precipitation is seasonal, falling between June and October, streams are ephemeral and restricted to scattered pools in the arroyos during the dry season. Nearly 90% of the forest is classified as tropical deciduous dry forest and is relatively short (10-15 m in height) and thickly distributed over the hills. A taller, semi-deciduous forest (15-25 m in height) occurs at lower elevations along the coast and extends inland along the arroyos. Land ownership is mainly protected private land (owned and managed by UNAM and Cuixmala Foundation), with a smaller proportion federally-owned (coastal and wetland areas).

Another area important for jaguars is the 1,396-km² RBSM straddling Jalisco and Colima. Elevations in this rugged area range from 360 to 2,900 m above sea level. Vegetation types include oak and pine forest and cloud forest. Camera-trapping surveys report low jaguar abundance, but abundant prey such as deer and peccary (Rodrigo Núñez-Pérez, Proyecto Jaguar, personal communication). Approximately 60% of the land ownership is ejido-communal and 40% is privately-owned, with 8,000-10,000 inhabitants inside the reserve and 32,000 in agricultural communities along its edges

(<http://www2.inecc.gob.mx/publicaciones/libros/2/manan.html>).

While not an officially-recognized protected area, the northern Jalisco coast, Cabo Corrientes Municipality, is also an important area for jaguars (Núñez-Pérez 2007). The land tenure in this area is mainly ejido and indigenous communities, with a smaller proportion privately-owned. Timber, extensive livestock operations, and subsistence agriculture are the main activities here.

In the RBCC, Núñez et al. (2000) and Núñez-Pérez (2006) used camera-trapping and telemetry studies to document jaguar and puma space use and diet, and Núñez-Pérez (2011) utilized camera traps to determine jaguar density estimates within the reserve. Núñez et al. (2000) and Núñez-Pérez (2006) determined that jaguars and pumas use the arroyos extensively, overlapping in both space and diet. Analyses of 50 jaguar and 65 puma scats identified the 4 main prey species of jaguars as white-tailed deer, collared peccary, coati, and armadillo (*Dasypus novemcinctus*), while the 5 main prey species of pumas were white-tailed deer, collared peccary, armadillo, black iguana (*Ctenosaurus pectinata*), and coati (Núñez et al. 2000). Average telemetry-based annual home ranges in this area were 110 km² for male jaguars, and 66 km² for females. Home ranges varied seasonally in size and sometimes in location (e.g., individual variation of 23.8 km² versus 38 km² and 56 km² versus 92 km² for females and males, for dry and wet seasons respectively; Núñez-Pérez 2006). Because jaguar home ranges and movements are more restricted during the dry season (due to the scattered and restricted nature of water sources during this time, which also influences prey availability), capturing photos of jaguars during this season may be more efficient (Núñez-Pérez 2006). Núñez-Pérez (2011) identified 8 individual jaguars from 26 photo-captures using 29 camera trap stations arranged in a polygon of 72 km². Using this information and information from telemetry work to estimate the effective sampling area, Núñez-Pérez (2011) determined density estimates of 4-5 jaguars/100km² in the RBCC.

Where jaguar and prey are protected in Jalisco, home ranges of both appear to be small, and likely smaller than in Sonora where more arid conditions and lower primary productivity may result in lower herbivore densities and larger jaguar home ranges. Home-range estimates for prey species are orders of magnitude smaller than jaguar home-range estimates. Collared peccary home ranges average 0.48-0.59 km² and range between 0.17-1.0 km² (Miranda et al. 2004). White-tailed deer home ranges average 0.4 km² (Sánchez-Rojas et al. 1997).

Núñez (in prep) has been using camera-trapping and social surveys to evaluate jaguar status and human-jaguar conflicts along the northern Jalisco coast, Cabo Corrientes Municipality. The questionnaire effort has covered 1,400 km² and the camera trapping has focused on 300 km² in the Comunidad Indígena de Santa Cruz del Tuito. This area is covered by tropical deciduous and semi-deciduous forest, with hilly terrain reaching elevations of about 1,000 m above sea level (Núñez in prep). The terrain is rugged, with arroyos separating prominent hills. Precipitation is 700-1,000 mm and seasonal, falling between June and October. Streams are ephemeral and restricted to scattered pools in the arroyos during the dry season. Deer, peccary, and coati are the most common prey species. Preliminary results indicate this area maintains a reproductive jaguar population (Núñez in prep), but further results regarding the jaguar's status and human-jaguar conflicts are not yet available.

Nayarit

In Nayarit, 2 sites have been surveyed in recent years: the RBMNN (Núñez and Vazquez 2013) and the [Área de Protección de Recursos Naturales](#) en la Sierra de Vallejo-Río Ameca (Núñez et al. in prep). The terrain in the 1,338 km² RBMNN, a wetland dominated by mangroves and swamps, is punctuated by ravines and coastal lagoons in the north of the Nayarit. In the south, the hilly 659 km² Sierra de Vallejo Biosphere Reserve includes a range of habitats including various statures of semi-deciduous forest, oak forest, and a 20 km² jaguar sanctuary. There are ongoing camera-trap and human-dimension surveys in the RBMNN (2011 to present) and in Sierra de Vallejo (Núñez et al. in prep). Both areas are considered [terrestrial conservation priority areas](#) by the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (National Commission on Biodiversity; CONABIO), include reproducing jaguar populations, and are national jaguar conservation priority areas. Elsewhere in Nayarit, areas like the Huicholes and Nayar have rugged mountains (250-1,900 m above sea level) that offer opportunities for jaguar conservation due to large areas lacking human populations. These 2 areas are in the process of being decreed as natural protected areas (http://www.conanp.gob.mx/que_hacemos/areas_prot.php).

Colima and Michoacán

Technically, the southern boundary of the NRU is in Colima, but the status of jaguars just south of that in Michoacán merit mention. Jaguar records are scarce for both Colima and Michoacán. The only recent data are from Michoacán and come from a part of La Sierra Madre del Sur covered by tropical dry and semi-deciduous forest, oak, and oak pine forest, with peak temperatures ranging from 29° C along the coast, 26° C in the Sierras, and 40° C in the Balsas Depression River, with annual precipitation ranging from 500 to 2,500 mm based largely on elevation (Núñez 2012). Recent jaguar records are from the southern part of the state (Charre-Medellín et al. 2013) and the abundance is relatively low (1.8 jaguar/100km²; Núñez-Pérez 2011, Núñez 2012).

PRESENCE-ABSENCE AND OCCUPANCY

Presence and distribution of species are important [state variables](#) in ecology and conservation. Occupancy surveys can be used to evaluate the spatial distribution or estimate the proportion of a given area occupied by jaguars and jaguar prey (MacKenzie et al. 2002, 2003, 2006). Occupancy models account for imperfect species detection, i.e., the fact that a sample unit might be occupied, but we fail to detect the species during our surveys. Occupancy surveys consist of detection/non-detection surveys conducted at a number of sample units (e.g., a grid cell or habitat fragment) over a number of repeated visits. In practice, a set of sampling units that is representative of the area of interest is surveyed repeatedly, using any method that allows detecting either the species itself or indirect signs of it, such as tracks or scats. Detection of the species of interest at each site during each repeat visit, or occasion, is recorded, resulting in a site-by-occasion data matrix, with entries of “1,” meaning the species was detected, and “0” if it was not detected. Multiple detections at a site-visit combination are condensed to a single entry of “1.”

To analyze these data, occupancy models combine a component describing whether or not a sample unit is occupied by the species of interest – this process is governed by the probability of occupancy, and, conditional on occupancy, whether or not the species is detected, governed by the probability of detection. Repeat visits to survey sites are necessary to inform this detectability model component.

Both probabilities (occupancy and detection) can be modelled as functions of covariates, such as habitat, climatic, or other variables. There are a range of different occupancy models, discussed briefly in the section [Types of Occupancy Models](#), the simplest being the single-season model. By model definition, in single-season models, occupancy at each survey site remains stable, i.e., it does not change during the survey (this is analogous to the “population closure” assumption in capture-recapture modelling). Detection probability, however, is allowed to vary and time-specific covariates can be included if deemed important. In addition, so-called multi-season (or dynamic) models are useful if you have data from surveys repeated over a longer time frame. These allow you to model changes in occupancy over time and investigate environmental drivers of local extinction and recolonization.

In this section of the survey protocol, we focus on the design of a single-season occupancy survey for jaguars in the core areas of the NRU. First, we discuss some general practical aspects of occupancy modelling. This is followed by specific suggestions of how to survey for jaguar occupancy in the core areas of the NRU. We finish with a brief discussion of analytical methods and ways to refine or adjust survey design.

Practical Considerations

Definition of occasion—Estimating the probability of detection requires repeated visits to each sample site. Camera-trap sampling is continuous (cameras are operational and collect data

throughout the entire study), such that the definition of an occasion is somewhat arbitrary. There are certain factors to be considered: occasions should not be chosen so short as to generate an overload of zeroes in the data set. This can cause detection probability to be close to 0, which in turn can lead to computational problems. On the other hand, overly long occasions will result in loss of information, because records are condensed to a binary format (detected or not) for each occasion. In situations where occupancy of low density animals in a sampling unit, such as a habitat fragment, is assessed with a single sampling point (e.g., a single camera trap), an occasion should be long enough to allow the 1 or few individuals occurring in the area to pass the camera and thereby be available for sampling during their movements through their territories. Occasion length should be held constant, but different lengths can be accommodated if necessary by including effort per occasion as a covariate on detection probability. Missing occasions, due to camera malfunctioning, for example, can also be accommodated during data analysis. Jaguar studies have used from 1 to 14 days as a single sampling occasion (Silver et al. 2004, Sollmann et al. 2012a). Seven days (1 week) may be an appropriate time period to consider as a sampling occasion for jaguars in the NRU, but the length of time for a single occasion can also be decided upon later once data has been collected (see section [Sampling Duration](#)). Sampling occasions may differ between portions of the NRU, given differences in jaguar density and home-range sizes (see [Jaguar Status and Habits in the NRU](#)). Differences in occasion length between portions of the NRU will not affect estimates of occupancy but will render estimations of detection non-comparable because they will refer to different timeframes. Given detection is simply a [nuisance parameter](#) requiring estimation to calculate occupancy, we suggest occasion length can differ between portions of the NRU if deemed necessary.

Definition of sampling units—Occupancy is a measure that refers to an area. Occupancy surveys, however, have been used extensively to sample continuous space (e.g., Linkie et al. 2007, Sollmann et al. 2012a). Surveying the designated core areas in the NRU for jaguar occupancy also qualifies as a survey in continuous space. In this situation, careful thought must be given to the definition of a sampling unit. To define the area a certain occupancy state refers to, researchers usually use a square, circle, or hexagon of the approximate home-range size of the species of interest (see [Spatial Autocorrelation](#)).

Allocation of effort—Accuracy and precision of parameters estimates – in the present case occupancy probability and its relationships with environmental covariates – are influenced by sample size. In occupancy surveys, sample size has 2 components, the number of sites surveyed and the number of repeat visits made to each site. Several studies have used simulation-based approaches to examine the trade-off between surveying more sites versus surveying more time. Overall, they found that the optimum strategy depends on detection and occupancy probabilities: when occupancy is low, more sites should be surveyed, whereas when occupancy is high, surveying fewer sites more often yields better results (Field et al. 2005, MacKenzie and Royle 2005). On the other hand, lower site numbers will limit the number of covariates that can be included in the model and will most likely affect the power of surveys to detect important

relationships between occupancy and covariates, or to detect temporal trends in occupancy (see also [Power Analysis](#)). Bailey et al. (2007) found that when surveying a higher number of sites for more repeat visits, model estimates were more robust to misspecification of the detection model (e.g., failure to include covariates on detection). MacKenzie et al. (2002) showed that increasing the number of sites surveyed, as well as the number of repeat surveys, resulted in better estimator properties. Similarly, O'Brien (2010) showed that if detection probability were low (0.02), even at high true occupancy values (60%), more than 100 sampling locations were necessary to achieve precise estimates ($CV < 20\%$). At double the detection probability, 60 sampling points were sufficient for adequate accuracy and precision. The number of sampling points necessary for good estimator properties increased at lower occupancy rates. In the case of camera trapping, repeat visits are generally not limited – once a camera is set up it will continue to collect detections until its battery or storage capacity is exhausted. Therefore, because large felids usually have low detection probabilities (due to low densities and elusive behavior), it seems advisable to aim for the maximum spatial coverage of the study area that financial and logistical constraints allow.

Spatial autocorrelation—Detections and occurrence of species are assumed to be spatially independent. In practical terms, that means that sampling units should be spaced far enough apart so that a single individual is unlikely to be recorded in more than 1 unit, usually at least the distance corresponding to a home-range diameter. Most frequently, this distance criterion is applied to the centers of neighboring sampling units. Spatial autocorrelation in occupancy can be taken into account by using autologistic or conditional autoregressive (CAR) modelling approaches (see [Types of Occupancy Models](#)). These models, however, are more complicated to implement and can have [convergence](#) problems. The effects of autocorrelation in occupancy, and the importance and best methods to formally account for spatial autocorrelation, are somewhat controversial (e.g., Dormann 2007). It seems most prudent to avoid spatial autocorrelation in occupancy whenever possible by using adequate spatial study design. Certain survey techniques can induce autocorrelation of detections. For example, when surveying for tracks along a road, using spatial (e.g., distinct trails or predetermined grid cells) rather than temporal repeats (e.g., searching an entire study site for a predetermined number of kilometers over a predetermined number of days [considered 1 encounter/capture occasion], and then repeat the search) can induce autocorrelation. Hines et al. (2010) developed a model that can account for this data structure.

Survey Protocol for Monitoring Jaguar Occupancy

The following survey protocol aims to evaluate and monitor jaguar occupancy across the core areas of the NRU over 15 years. We focus on suggestions for a single-season survey, but also provide guidance on how to evaluate the power of multi-season surveys to detect changes in occupancy. Our recommendations are based on experiences of the authors with survey and analytical methodologies, as well as with jaguar ecology and logistical concerns in the NRU. It should be noted that we developed suggestions without specific consideration of budgetary

constraints. Further, we believe that the suggested study design can be refined based on a thorough review of existing jaguar occurrence data and/or smaller scale pilot studies. We touch on all of these issues in the following sections.

Defining and Choosing Sample Units

In occupancy analysis, the sampling unit is a location or area where data are gathered with an assumed outcome of either a species detection or non-detection by 1 or more detection devices in each sampling unit (MacKenzie et al. 2006, Long and Zielinski 2008). MacKenzie et al. (2006) suggested a sampling unit should be large enough to have a reasonable probability of the species being there (i.e., a probability between 0.2 and 0.8), but small enough so any measure of occupancy is meaningful and the site can be surveyed with a reasonable level of effort. Thus, sample unit areas are often based on the largest home-range estimates of the target species.

Gutiérrez-González et al. (2012) estimated jaguar densities of 1.05/100 km² in the NJR. Rosas-Rosas and Bender (2012) estimated jaguar densities at 1/100 km² in the Alianza para la Conservación del Jaguar en la Sierra Alta de Sonora UMA. Moreno et al. (2013) estimated 2.7 jaguars/100 km² in the Sierra Madre Mountains of northeastern Sonora. Núñez-Pérez (2011) estimated jaguar densities of 4-5/100 km² in Chamela-Cuixmala Biosphere Reserve in Jalisco, likely the highest reasonable estimate from the NRU, in an area where male home ranges averaged 110 km² (Núñez-Pérez 2006).

Estimates from several other areas include densities of 5.7-5.8/100 km² and male home ranges of 140-170 km² in the fertile and well-watered flood plains of the Pantanal (Soisalo and Cavalcanti 2006, Cavalcanti and Gese 2009); densities of 2.47/100 km² and male home ranges of 280-299 km² in the humid Atlantic forest of Brazil (Cullen Jr 2006); and from the low stature and often dry and hot forests of the Chaco near the southern limit of jaguar range, densities (averaged over 10 surveys) in Bolivian Chaco of 0.866/100 km² (Noss et al. 2012), with male home ranges in the Paraguayan Chaco of 692 km² (McBride 2009).

Because published information on the scale of home ranges in the NRU is limited, some guesswork is required to assign an appropriate sampling scale for an efficient occupancy survey. As a reference, 2 density estimates from Sonora (Gutiérrez-González et al. 2012, Rosas-Rosas and Bender 2012) are less than half those in the Atlantic forests of Brazil, where male home ranges average nearly 300 km² (Cullen Jr 2006), yet higher than in the Chaco (Noss et al. 2012), where male home ranges can average nearly 700 km² (McBride 2009). Our expectation is that on a large scale jaguar densities are low in Sonora and home ranges are large. We recommend hexagons of 500 km² as the sample units across the NRU. To survey a representative set of units, we suggest overlaying a grid of 500-km² hexagons on the NRU ([Figure 3](#)), then surveying 50% of the resulting hexagons to ensure sufficient data are collected for reliable occupancy modeling. These units can be chosen completely randomly, or, preferably, systematically with a random starting point. This second option will result in better spatial coverage of the overall area of

interest. Following this approach, the Sonora Core Area consists of 155 hexagons ([Figure 4](#)), 78 of which should be sampled, while the Jalisco Core Area consists of 109 hexagons, 55 of which should be sampled. In addition to these core area hexagons, we suggest choosing additional sample units beyond the border of the core areas to investigate possible range expansion or contraction. Despite probable variation in home-range sizes between Jalisco and Sonora, we suggest using the same sampling units to maintain comparability of surveys between the 2 core areas.

When designing studies in other parts of the jaguar's range, similar considerations should apply; sample units (cells) should be tailored by knowledge or estimates of local jaguar home-range size to reduce auto-correlation and assess occupancy in a biologically meaningful way. Depending on the outcome of the initial survey, it is conceivable that spatial coverage of the core areas in subsequent surveys could be reduced to 30% of all hexagons, but this option should be evaluated carefully based on the data and study objectives (see [Power Analysis](#)).

Spatial Coverage of the Sample Unit

Each hexagon should be sampled with 5 camera trap stations ([Figure 5](#); see [Setting Cameras](#)), with 1 camera per station (see [Setting and Checking Cameras](#)). This represents a compromise between achieving spatial coverage of the sample unit and maintaining logistical feasibility. If more manpower and cameras are available, an additional 2 cameras can be installed in the sample unit, in the event some of the cameras malfunction or are stolen. Cameras should be installed in a regular grid within a hexagon for optimal spatial coverage (e.g., [Figure 6](#)). This arrangement is easily adjustable to other numbers of cameras. This regular grid should be understood as a guideline for where to set up cameras within the hexagon; specific locations should be chosen to optimize jaguar detection probability (see [Setting Cameras](#)).

Sampling Duration

Single-season occupancy models assume that the occupancy state at each sampling unit does not change over the course of the survey. Therefore, survey duration should be limited to a time frame that ecologically approximates this assumption. For a large-scale survey like the one suggested here, logistics, the necessity to acquire sufficient data for modelling, and the closure assumption must be weighed against each other. Based on experience of some authors with camera trapping in the NRU, approximately 3 months will be required for camera set up and retrieval (see also [Logistical Challenges](#)). We suggest sampling at each site for 3 months to acquire sufficient data. Logistical constraints make it impossible to set up all cameras throughout the NRU in 1 or a few days. Therefore, considering the entire NRU, camera traps will be set up successively throughout the study area. We suggest an overall survey duration – from the first camera's first day to the last camera's last day – of 6 months. This period could be subdivided into 24 1-week sampling occasions, 18 10-day sampling occasions, or 12 2-week sampling occasions. As mentioned before, defining occasions in a continuous survey is somewhat

arbitrary, and occasion length can be adjusted depending on the data at hand (see [Practical Considerations – Definition of occasion](#)). Overall survey length could also potentially be reduced if sufficient detections were obtained in a shorter time frame, or extended, if data appear to be too sparse. As a frame of reference, in areas known to hold jaguar populations in the Sonora Core Area, it takes approximately 2 weeks to record the species for the first time (Carlos López-González, Northern Rockies Conservation Cooperative, personal communication). Because setting up camera traps is time consuming and logistically challenging, it will be beneficial to leave camera traps in the field as long as the equipment and the constant occupancy assumption permit.

We further suggest sampling over the course of the dry season, to avoid camera-trap malfunctions related to rain/humidity and logistical difficulties due to inclement weather. Constraining the survey to a single season will also help approximate constant occupancy states. In Jalisco, the dry season lasts from October to May, in Sonora from November to June.

Setting Cameras

The approximate location of a camera trap will be determined in the lab using GIS software, following the approach outlined above. When in the field, however, these locations need to be adjusted to suitable spots for camera-trap setup. Jaguars are known to travel preferentially along small dirt roads and trails (Salom-Pérez et al. 2007, Sollmann et al. 2011), males more so than females (Conde et al. 2010). Therefore, camera traps for large cats are frequently placed along roads or other landscape features (like arroyos or washes) that provide easy movement paths and “funnel” the animals in front of the camera. These features, and other micro-habitat characteristics of the setup location, likely influence detection probabilities. The more the landscape funnels the animal towards the camera, the higher the chance to record it when it is in the area. Therefore, clear travel routes (trails, roads, rivers, or other habitat edges) in overall more closed habitat often have higher detection probabilities than cameras placed in open habitat with little structure and where animal movement is less constrained. The specific setup situation should therefore be carefully documented.

A standardized protocol should be developed beforehand by people familiar with the study area, including clear descriptions of the features to be recorded. This will ensure that data are collected systematically. Characteristics should include, but are not limited to, presence of a road or trail along which the camera is set up, width of the trail or road, presence of another kind of habitat edge (e.g., grassland/scrubland), presence of a stream/river, mountain ridge, or gully along which the camera is set up, density of habitat surrounding the camera (e.g., can animals move around freely or are they likely to stay to defined paths), canopy cover, etc. For data organization and storage, see [Data Recording](#). Local residents can be of great help when it comes to finding suitable spots to set up camera traps, as they might know of locations where tracks or other sign of jaguars have been seen before. Guidance on collecting data from incidental observations of

jaguars is provided in [Appendix 4](#). Guidance for collecting data on tracks and scats encountered in the field is provided in [Appendix 5](#).

Below are suggestions for setting camera traps for jaguars adjusted from the literature review by Polisar et al. (2014). See [Figure 7-8](#) for photographs illustrating the setting of a camera trap and a photograph of a jaguar captured by a camera trap.

- Find a spot where there is a suitable tree or post. 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. In open areas, it might be necessary to bring appropriate stakes into the field to set up camera traps in suitable spots without being restricted by the presence of appropriate trees. Try to minimize direct sunlight on the cameras, as excessive heat can reduce the sensitivity of the sensors to warm-blooded animals and/or create false triggers when clouds block the sun. Cameras should be set back at least 2 m 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. Because the sensor beam should be approximately shoulder high, for a jaguar the camera should be set approximately 50 cm off the ground and parallel to it.
- Once the camera is set, clear the area between the camera and the path of travel of all vegetation that obstructs the beam or the field of view of the camera. Leaves and vegetation that are easily windblown 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 the camera by passing in front of it. 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 1 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 2010). Especially in the Sonora Core Area of the NRU, presence of cattle and their frequent triggering of camera traps need to be taken into account.
- Some studies have used scent attractants such as Calvin Klein's Obsession®, Chanel N° 5® (original or imitations), or predator scent lures to attract jaguars into the camera's sensor field. The lure can be sprayed on a piece of fabric or tampon attached to a stick, protected either by a cut-off plastic bottle or in a small baby food jar with the top sealed with tape but punctured with fine holes, which prevents animals from removing the lure or rain from washing it away while allowing the scent to dissipate in the air. The device is

then fixed in or above the ground in the center of the camera's sensor field. The scent has to be replenished regularly, which may pose a problem in logistically challenging environments. 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, García-Anleu 2012, Isasi-Catalá 2012). If the lure cannot be replaced frequently enough to ensure constant coverage, there is the possibility that, as the scent wears off, detection probability decreases. Because occupancy modeling does not rely on individual identification, application of a lure is not essential, and not using any attractant may be an easier option where lure cannot be replaced frequently.

Data Recording

Photographic records—All photographic records should be entered into a comprehensive database with a single line for every independent record of every species, including humans and domestic animals (see Sunarto et al. 2013 for an example of a Microsoft Excel spreadsheet). Data can easily be reduced to a detection/non-detection format for jaguars or other species of interest. This basic format also provides flexibility to adjust occasion length after the survey has been completed. Information associated with each record should include, but is not limited to, species, individual identification, sex and age if possible, number of individuals in the picture, time of day, date, camera-trap station identifier and/or coordinates, study site, and survey identifier (if multiple surveys are run in a study site). For ease of post-processing, nomenclature and spelling of entries, including missing values, should be standardized.

Photographs should be stored in a manner that makes locating a specific record easy, e.g., in a folder structure that identifies the camera trap site and date range. Specific software is available to store camera-trap data and link spreadsheet records to photographs. For example, Camera Base (<http://www.atrium-biodiversity.org/tools/camerabase/>) extracts metadata (time, date, etc.) from digital images, allows batch read-in of pictures from secure digital (SD) cards, and includes functions to extract certain data formats from the database, such as capture-recapture detection histories or activity patterns. DeskTEAM (<http://www.teamnetwork.org/>) is another platform for camera-trap data entry, from trap deployment to photographs and their associated information; a new version based on open source database management systems is currently being developed. General photo handling software such as ExifPro (<http://www.exifpro.com/>) can also be used to manage camera-trap pictures. Ultimately, as long as the same information is stored, it is up to the researchers' preference which system to use for data storage.

Regardless of the chosen platforms to manage and archive data, we provide a standardized spreadsheet for jaguar detections in [Figure 9](#). This spreadsheet is designed for compatibility with the Jaguar Event-Record Database (<http://jaguardata.info/>) developed by WCS. The necessary user interface for easy batch import of jaguar observations from camera-trap data (and other data sources) using this standard spreadsheet could be developed to increase the time and efficiency

with which large datasets from camera trapping or telemetry could be incorporated into the existing database. Importing jaguar observations into this overall presence database will help centralize information on jaguar occurrence and allow researchers to find out about jaguar studies throughout the species' range.

Survey information—In addition to the actual camera-trap data, it is important to keep track of survey related information, such as camera-trap location (in latitude and longitude), date of installation and retrieval, and local characteristics of camera setup (see [Setting Cameras](#)). If upon checking or retrieving a camera trap, the unit is not working (because it is malfunctioning, out of battery, out of storage space, or vandalized), this should be recorded. Often, the date of the last record on that particular camera trap is used as an approximation of the last day the unit was working. Taking test pictures using a trigger card that has the station code, date, and time, when installing, checking, and retrieving cameras, helps keep track of camera functioning and aids in organizing and labeling of the large number of folders of camera-trap data. Some cameras can also be programmed to take a picture every day without an external trigger, which can later be used to determine any days the camera was not functioning. Once the survey is completed, a survey effort spreadsheet for all cameras should be constructed, with a line for each camera-trap station and a column for each day of the survey, from the day the first camera was set up to the day the last camera was removed, with entries of “0” or “1,” depending on whether a given camera trap was installed and working on any given day (1) or not (0).

Covariates—Both occupancy probability and detection probability can be modeled as functions of covariates. In single-season occupancy models, occupancy probability can only be a function of spatial covariates. If the objectives of the study include predicting occupancy to non-sampled areas, covariates need to be available for the entire area of interest (here, the core areas of the NRU), not only for the actual camera-trap sites. This generally limits possible covariates to remotely sensed or other GIS-based data, or covariates from some area-wide census data (settlements, roads, human population density, etc.), because covariates collected in-situ around camera traps will not be available for the larger area of interest. Detection probability can be modeled as a function of location-specific and time-specific covariates. If the latter is of interest, the covariates matrix also needs to include a section with site-by-date values of covariates varying with time, such as rainfall, temperature, etc. Because extrapolation of occupancy probability to non-sampled areas does not require extrapolation of detection probability, spatial covariates on detection can be collected in-situ. Examples for such covariates are given in the section [Setting Cameras](#).

Occupancy model input data format—Depending on which software is used for implementing occupancy models, the structure of the input files might vary slightly. The general idea, however, is the same across analytical platforms: the input data consists of a site-by-occasion detection/non-detection matrix for the species of interest; a matrix with site-specific habitat covariates; and site- and occasion-specific time-dependent detection covariates (some programs might require a separate matrix for occupancy covariates and detection covariates). Some

programs, such as Camera Base, allow you to extract the detection/non-detection matrix automatically from the database. The free software R (R Core Team 2014) is another option to manipulate the raw data matrix easily and repeatedly.

Data Analysis

A number of platforms exist for analysis of occupancy survey data. PRESENCE (Hines 2014) provides an easy-to-use interface for data input, model building, and reading output. Plenty of documentation and working examples are available online. For people familiar with the program R, the package “unmarked” (Fiske and Chandler 2011) provides a range of functions for occupancy modelling. Both PRESENCE and R/unmarked implement occupancy models in an Information Theoretic framework. Implementing occupancy models in a [Bayesian framework](#) is straightforward using programs such as WinBUGS (Gilks et al. 1994) or JAGS (Plummer 2003). Kéry (2010) and Kéry and Schaub (2012) provide easily accessible introductions to using these programs for ecological analyses including occupancy modelling. These platforms afford the user additional flexibility in model building. In addition, for certain models, Bayesian implementation is easier. For a brief discussion of useful types of occupancy models see section [Occupancy Modelling](#).

Equipment and Costs

Personnel—Field work should always be conducted in teams of at least 2. A field assistant will cost approximately 750 USD per month in salary. As a frame of reference, in a 300-km² survey of Mexican wolves and their prey, 3 teams spent 3 days in the field to set up 30 camera traps (Carlos López González, University of Querétaro, personal communication). This translates to 1 team-day (i.e., 1 team working 1 day) per 3.3 camera traps. Scaled up to the suggested design, the core-area-wide survey would require approximately 118 team-days for Sonora (78 hexagons times 5 cameras) and 83 team-days for Jalisco (55 hexagons times 5 cameras) for installing camera traps. Camera retrieval will likely be faster, but nevertheless requires additional team-days. The costs estimated here do not include vehicle purchase or rental, or vehicle running costs, which for a study this large may be substantial. Also, the amount of person-hours needed to identify species on photographs and transfer the photo-records into a database after the survey has been concluded should also be taken into account.

Camera traps—Depending on the model, camera traps (including storage card, cable, and lock) cost between 250-450 USD. For each core area, a full study would require approximately 500 cameras, including cameras for additional hexagons along the core area border, and back-up units to replace malfunctioning cameras. Depending on the specific model, this results in a total cost for camera traps of 125,000-225,000 USD. There are many different brands constantly developing new models, such that it is not feasible to provide a comprehensive review of current models without the list being outdated almost immediately. We suggest checking user reviews of different brands and models available at www.trailcampro.com.

Different models come equipped with a range of functions. Two fundamental camera features to consider are the kind of sensor and the kind of flash. Most camera traps come with a passive infrared heat-in-motion sensor. These are activated as a warm-blooded animal walks through the sensor field. There are, however, models with active infrared beams (most notably, Trailmaster® cameras). These cameras are triggered when an animal (or any object) breaks the beam. They require setup of a transmitting and a receiving unit on opposite sides of the trail or focal point, which can be more complicated. The great advantage of active traps is that they are not triggered by mere sunlight. A falling leaf or heavy rain, however, will activate the camera if it breaks the infrared beam (although a minimum beam break time can be programmed).

Modern camera traps are available either with white-light or infrared flash. White light provides sharp, colored night-time pictures, which increases the chance of individual identification. This is not necessary for occupancy modeling, but would provide additional information on the minimum number of jaguars in the landscape and individual movements. On the other hand, white light alerts people to the camera's presence and may increase the risk of theft; additionally, some studies have argued that the flash may induce a behavioral response to the device (Wegge et al. 2004). Finally, white flash usually requires some time to recharge, so that minimum time intervals between subsequent pictures may be longer (in the order of seconds). However, some models have circumvented this limitation by having the flash stay on for the duration of the number of photos taken per trigger event. In contrast, infrared flash does not "freeze" the object in motion and therefore may result in blurry pictures, allowing species identification but complicating identification of details (individual, sex), especially for animals walking quickly past the camera. Scent devices can be installed to slow cats down in front of the camera to increase the chance of a high quality, non-blurry picture allowing for individual identification even with infrared flash (see [Setting Cameras](#) for details). In addition, a number of sequential pictures can be taken to improve identification success.

Others—Camera traps should be equipped with 16 gigabyte (GB) memory cards. These should provide sufficient storage capacity for 3 months, even in areas where cattle may frequently trigger the camera. In areas with human presence, it might be advisable to install cameras inside metal boxes that can be locked to a tree or post using a cable lock. Battery needs (size, type, quantity) will depend on the camera-trap model and survey duration. Additional equipment needed for camera-trap surveys includes global positioning systems (GPS) units, tools to remove vegetation, and possibly others. With a large-sized study like the present one, costs for these additional items need to be taken into account.

Logistical Challenges

A major component of implementing a large-scale survey in the Sonora and Jalisco Core Areas is the contact and communication with landowners. Due to the local land tenure system, each hexagon in northern Sonora can be expected to consist of at least 15-20 independent properties. In southern Sonora and Jalisco this number increases to approximately 400 (Carlos López

González, University of Querétaro and Rodrigo Núñez-Perez, Proyecto Jaguar, personal communication). Establishing contact with landowners to obtain permission to access their land and set up a camera trap on it is not necessarily straightforward. Especially in Sonora, many landowners spend large parts of the year elsewhere. The staff generally does not provide their employer's address or phone number, nor are they in the position to grant permission themselves. To streamline the actual camera-trap survey, permissions to work on private lands should ideally be obtained before camera installation begins. This will require extensive preparatory work and is the most challenging logistical aspect of implementing a large-scale study in this landscape.

Occupancy Modeling

Types of Occupancy Models

Occupancy modeling has a flexible framework and includes a number of different models. The simplest one, and the one we have focused the present document on so far, is the single-season occupancy model, where occupancy remains constant during the study. This model can be extended to multiple surveys, where occupancy is allowed to change from one survey to the other; to multiple states, for example “absent” versus “present but rare” versus “present and abundant”; and multiple species or community models. The Royle-Nichols model (Royle and Nichols 2003) makes use of the link between abundance and detection probability to estimate local abundance of focal species. Other classes of occupancy models deal with situations where either the occupancy state or the detections are thought to be spatially correlated. This is by no means an exhaustive list, and different frameworks can be combined with each other (for example, multi-state models can be combined with multi-season models). But the following models are those that we deem most useful for the purpose of monitoring jaguar (and prey) occupancy in the NRU. In this section, we provide brief outlines of these models. We refer the reader to the extensive literature that exists on these models for further details (Polisar et al. 2014).

Single-season models—This is the basic occupancy model described briefly in the [Background](#) section, which allows for simultaneous estimation of the probability of occupancy and the detection probability (MacKenzie et al. 2002). Occupancy and detection parameters may be constant across the sampling area or can be estimated as functions of site- and survey-specific covariates (the latter only for detection). Random effects can be used to deal with unobservable heterogeneity, resulting in so-called mixture models. 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 estimate occupancy for sites that were not sampled, but fall within the study area and have the same type of covariate information as the sampled sites.

Multi-season models—These 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 from occupied to unoccupied between seasons. These processes are governed by probabilities of local extinction and colonization, which are estimated within the model. We discuss these models in more detail in the section on [Measuring Trends in Occupancy](#).

Multi-state models—These 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, occupancy models can be used to estimate if a species is absent, rare, or abundant, or, alternatively, if different life history stages are present, such as: absent, present, breeding/reproducing. These models can incorporate uncertainty in state observations (Nichols et al. 2007) and can also be extended to multiple seasons (Mackenzie et al. 2009).

Multi-species model—These models combine detection/non-detection data from a community of species to estimate both species-level and community-level parameters (Dorazio and Royle 2005, Dorazio et al. 2006). Essentially, they are a form of mixed (or random effects) model, where species-level parameters are assumed to have a common underlying distribution that is governed by community-level parameters. In that manner, information is shared across species and even species that are rarely detected (and therefore cannot be modeled independently) can be incorporated in the analysis. These models can be of interest to model the medium- to large-sized terrestrial mammal community from camera-trapping data, which constitutes the prey community for jaguars.

Abundance-induced heterogeneity (Royle-Nichols) models—These models are based on the idea that heterogeneity in abundance generates heterogeneity in detection probability (Royle and Nichols 2003), i.e., the more locally abundant a species, the easier it is to detect at least 1 individual of that species during a survey. Based on this concept, the Royle-Nichols model uses detection/non-detection data to estimate point abundance of the focal species. This model may be of particular interest to model prey abundance, because most prey species cannot be individually identified.

Models for autocorrelation in detection—These models are used when we have correlated observations, either spatially or temporally, violating the assumption of independence of detections (Hines et al. 2010). For example, when conducting sign surveys along trails, we may detect the same individual repeatedly along the survey transect, leading to spatially autocorrelated detections. Ignoring this data structure can lead to [biased](#) estimates of occupancy. The model developed by Hines et al. (2010) subdivides transects into segments and uses a first order Markov process to describe dependency of detection in 1 segment conditional on detection in the previous segment to yield unbiased estimates of occupancy. The trail/sign survey example deals with spatial replicates, but a similar data structure can arise if temporal replicates are not independent of each other.

Models for autocorrelation in occupancy—The above described model for autocorrelation deals with the situation where detections are not independent from each other. But occupancy models also assume that species occurrence at the different sample sites are independent of each other. This assumption can be violated if sample sites are too close to each other so that a single individual can occur at more than 1 site. The survey design we outlined in the present document attempts to avoid this issue by choosing sampling units on the scale of a home range. But additional, finer scale information on jaguar habitat use can be obtained from this survey design when we consider within-hexagon camera stations as sample units (in contrast, in the suggested design outlined in this protocol, each hexagon is a sample unit). Given the species' large movements, we cannot consider these within-hexagon camera stations to be fully independent of each other. The most common ways to account for spatial autocorrelation are by using: 1) an autologistics regression type of occupancy model, where occupancy at a given site is a function of occupancy at neighboring sites; or 2) by using a conditional autoregressive (CAR) model (Besag et al. 1991), where a spatially correlated error term is added to the predictor of occupancy probability. In both cases, the neighborhood of a given site can be defined based on knowledge of the species' movements (e.g., Mohamed et al. 2013) or based on analysis of residuals (Moore and Swihart 2005, Sollmann et al. 2012a). Autologistic and CAR models are most easily fit in a Bayesian framework.

Pilot Data

The suggested survey is a logistically and financially challenging endeavor. It seems wise to conduct some smaller-scale pilot studies to assess the feasibility and reliability of the outlined survey approach. Such pilot studies could be implemented in 1 or a few hexagons, following the setup and design recommendations outlined in this document, and could be carried out in different regions of the NRU. Although the collected data would likely not be suitable for occupancy (or other) modeling, it would provide information that could be used to parameterize data simulations for a simulation-based assessment of the accuracy and precision of estimates under different sampling scenarios (see [Power Analysis](#); for examples of such assessments, see MacKenzie and Royle 2005, Bailey et al. 2007). Alternatively, or in addition, existing camera-trapping data could be compiled and used in an analogous fashion, allowing refinement of the survey protocol. In addition to scientific and gray literature, the Jaguar Event-Record Database (<http://jaguardata.info/>) provides a reasonable starting point for compiling existing information on jaguar presence and detection.

Measuring Trends in Occupancy

One major objective of the occupancy survey outlined in this protocol is to support assessment of the jaguar recovery criteria, which include an increase in (or at least stability of) occupancy. Multi-season occupancy models provide the opportunity to explicitly model changes in occupancy from one survey/season to the next. The design for a multi-season (also called dynamic) occupancy model is the same as for a single-season one, but the single-season survey is

repeated at certain larger time intervals. This reflects the “robust design” idea developed by Pollock (1982) in the framework of capture-recapture models, where a survey is repeated over T [primary occasions](#) (seasons, years, etc.), and within each primary occasions there are repeat visits to sample sites – so-called secondary occasions. Occupancy remains constant within a primary occasion (across secondary occasions), but is allowed to change between primary occasions. Occupancy in the first primary occasion ($t = 1$) is modeled as in a single-season occupancy model; in subsequent occasions, it becomes a function of occupancy in the previous year: if a site was occupied at time t , it can either become unoccupied at time $t + 1$ (local extinction), with probability ϵ (extinction probability), or remain occupied (with probability $1 - \epsilon$). A site that was unoccupied at time t can either become occupied at time $t + 1$ (recolonization) with probability γ (recolonization probability), or remain unoccupied (with probability $1 - \gamma$). Both ϵ and γ can be modeled as functions of spatial and temporal covariates, but accurate and precise estimation of these parameters generally requires a reasonable number of primary occasions (Bailey et al. 2007).

As an alternative to modeling these mechanisms explicitly, data from several surveys can be combined and a time effect can be included in the predictor for occupancy. A positive coefficient for time would indicate an increase in occupancy probability. Again, to detect a significant effect will likely require a reasonable number of seasons/surveys. The necessary number of primary occasions can be determined (at least approximately) using the approach outlined in the section on [Power Analysis](#). Such an approach might be of interest to determine how often and at which intervals the outlined survey would have to be repeated to detect changes in occupancy as outlined in the Recovery Criteria.

Power Analysis

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 a certain study design 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).

Depending on the objectives of a study, it might be better to detect false change rather than missing a change. For example, when dealing with a critically endangered species, it might be more prudent to accept higher type-1 error rates (e.g., Hayward et al. 2002). Having a clear understanding of what the study objective is and what level of power or error is acceptable are crucial to performing a power analysis.

Power analyses are often performed using simulation-based methods, following some basic steps (adjusted from Bailey et al. 2007):

1. Define model of interest (single-seasons, multi-season, etc.);

2. Define sample design for which power is being investigated (number of sites, number of repeat visits, etc.);
3. Parameterize the model (define true values of detection probability, occupancy probability, covariate relationships, etc.) – this step requires information from pilot studies or studies carried out under similar circumstances/on similar species;
4. Generate detection/non-detection data from model;
5. Analyze simulated data with model under consideration;
6. Extract parameter estimates, measures of uncertainty/variance, and bias;
7. Repeat steps 5 and 6 for a large number of times;
8. Summarize results to assess average bias and precision.

For occupancy models, both single-season and multi-season, the program GENPRES (Bailey et al. 2007, Hines 2014) lets users perform such power analyses, as well as analyses of other aspects that might impact accuracy and precision of parameter estimates.

Occupancy Modeling for Prey Species

Camera traps collect a wealth of data on non-target species, including potential mammalian prey species for the jaguar. In the NRU, such species include white-tailed deer, collared peccaries, armadillos, and others (Núñez et al. 2000, Rosas-Rosas et al. 2010). Most of these species have much smaller home ranges than jaguars, so the above suggested spacing of camera traps *within* hexagons should be wide enough to provide or approximate spatially independent survey locations. Under these circumstances, the photographic data can be used to model prey occupancy, using the methods outlined above. Analogous to the jaguar, prey occupancy could be predicted for the NRU, and potentially serve as an explanatory variable to predict jaguar occurrence.

To account for the presence of a range of prey species, binary criteria can be developed, such as “at least an $X\%$ chance of Y prey species occurring.” It should be noted that the camera-trap setup suggested above attempts to maximize jaguar detections, and will not necessarily optimize detection for other species, based on 2 factors. First, prey home ranges are small in the NRU, and in some cases will be much less than the approximately 100 km^2 sampling accomplished by 5 camera traps distributed across 500 km^2 . Second, several herbivores have been shown to have higher detection probabilities off of roads (e.g., Harmsen et al. 2010), either because of different movement patterns, or because of active avoidance of carnivore travel paths. The suggested study design could potentially be adjusted in several ways to increase detections of target prey species. For example, if logistics, equipment, and manpower permit, additional cameras could be added to the existing camera-trap stations (or to some of them) and placed in a manner that optimizes detection of species that do not travel preferentially on roads. Differences in setup

would have to be accounted for in the analysis. Alternatively, if the existing survey design is extremely efficient in detecting jaguars in hexagons, some of the stations in each hexagon could be set up to target prey. If home ranges for prey species with large movements (such as peccaries) are in excess of 100 km², then occupancy analysis using camera stations as sample sites might have to account for spatial autocorrelation in occupancy, as outlined in the section [Types of Occupancy Models](#), or use hexagons as sampling units. The Royle-Nichols model for abundance-induced heterogeneity in detection is of particular interest for prey species, as these generally cannot be identified to the individual level for capture-recapture analysis.

Hines et al. (2010) designed and Karanth et al. (2011a) tested a model that could accommodate serial, spatially-replicated sign-based occupancy sampling across a 38,000-km² landscape that included 21,167 km² of potential tiger (*Panthera tigris*) habitat, including 5,500 km² of wildlife reserves. Roads and trails made active searches for sign feasible in this test of tiger occupancy. On a spectrum of efficiency, when study areas have good access and a system of roads and trails, an active search for sign will collect more data, more quickly, and more comprehensively, at the presence-absence level, than camera traps. Rather than waiting for jaguars to pass, biologists can quickly cover many kilometers and find where jaguars have passed, generating data faster. The limitations of universal application of this method with large cats and most prey include rocky, mountainous substrates, hard clay substrates, deep forest litter, and a complete lack of any road and trail system; all are quite common conditions in the jaguar's range. On substrates which yield no tracks, and areas with few roads and trails, camera traps will be more efficient. The semi-arid, often rocky habitats of the northern portion of the NRU fit the latter description; thus, camera traps are a logical choice.

Because camera traps passively wait in space for resident and transient jaguars to pass, an alternative design might consider elevating the “search” by moving the camera traps halfway through a large scale study. Intuitively, the outlined design of 5 camera traps simultaneously sampling has a passive spatial component, and a temporal component bounded by arbitrary occasions (a range of occasion lengths can be considered). Standardized moves halfway through a study might add data with 2 sets of sequential occasions and a more comprehensive search of the area. Increased staff familiarity with a cell as units are checked in time A might suggest alternative sites for time B, which then could be sampled with no increased equipment, minimal additional labor costs, and perhaps a biologically more accurate assessment of jaguars and prey across a large cell. Alternatively, the semi-systematic allocation of stations depicted in [Figure 6](#) could guide switches into additional “pie segments” of a hexagon, more comprehensively providing opportunities for jaguar detection, and more closely approximating prey home ranges. During analyses, the 2 different sample times would both be sequential from day 1 using identical occasion lengths. This might represent a trade-off between length of occasion and/or depth of resampled occasions to generate detection histories, and greater opportunities to intersect jaguars in space. Duration of sampling could be adjusted accordingly.

Sign-based Occupancy Sampling for Jaguars

Some parts of the jaguar's range do possess characteristics that may allow efficient serial sign surveys as the basis for occupancy modeling design suggestions (due to road systems, semi-open habitats, or dropping water levels along river and lake beds at onset of the dry season, for example). We offer interpretations based on the work of Karanth et al. (2011a) and Gopalaswamy (2012a) on tigers and their prey for areas with these characteristics.

Sample area: Predicted and potential occupied habitat within the area of interest based on previous mapping and modeling, excluding all areas judged unsuitable.

Cell size: An area which is on average larger than an estimated maximum male jaguar home range.

Season: That which provides maximum sign availability in the study area (the end of the rainy season can be good due to moist substrates and dropping water levels).

Allocation of effort: Because the cell size may be large, and therefore sampling may be physically and logistically intensive, a sampling design covering representative proportions of the study area might be required (30-50% of cells as suggested in camera-trap based occupancy design).

Within cell sampling: Skilled and experienced trackers who have received training in the standardized methods conduct transects composed of connected serial 1-km sections, starting from or passing through a randomly located point in the cell. Sampling within the cell is proportional to habitat availability, excluding sample areas that are not jaguar habitat. All detected sign types are recorded at 1 time only (present-absent) within 100 m intervals (jaguar, conspecific carnivores, potential prey, livestock, humans) along with a habitat classification, according to a predetermined template for data collection. All sign is photographed, recorded, and geo-referenced.

Modelling and analysis of data: Use the Hines et al. (2010) refinement of the standard occupancy model (MacKenzie et al. 2002) to deal with Markovian dependence of animal sign detections on spatial replicates as outlined in Karanth et al. (2011a). The sign can be aggregated at 1-2 km intervals to form spatial replicates within the sample cell. It may be logical to aggregate at finer levels for smaller prey to more biologically accurately reflect their level of occupancy (e.g., 500 m or 200 m). Disjunct trail segments due to habitat unsuitability can be combined sequentially (Karanth et al. 2011a). The cell-specific occupancy parameter should be weighed by the proportion of potential jaguar habitat in each cell. The "prey-density covariates" for each cell can be the proportion of 1-km replicates containing sign of each prey species (Karanth et al. 2011a), although a more finely tuned assessment according to shorter segments can be considered. Karanth et al. (2011a) used livestock as a proxy for human-disturbance. The same interpretation merits exploration in jaguar habitat. Because jaguar densities are high in

some high livestock biomass areas, remote sensing additional covariates can and should be added (such as distance to human settlement, presence of water bodies, distance to water, habitat type, topography).

Sign-based occupancy studies by Sunarto et al. (2012) on tigers in Sumatra serve as a useful example for sign-based jaguar occupancy surveys. Field staff recorded tiger detections and habitat variables along 100-m segments along 40, 1-km transects in each of 47, 17 km x 17 km grid cells (Sunarto et al. 2012). These nested designs (Karanth et al. 2011a, Sunarto et al. 2012) allow estimates of the probability of large cat occupancy at a large landscape level (e.g., large landscape grid of 17 km x 17 km = 289 km² cells in the Sunarto et al. (2012) tiger study in Sumatra, and 188 km² in the Karanth et al. (2011a) tiger study in a prey rich habitat in India) and also the probability of habitat use at the finer level based on the data recorded in 100-m segments along 1-km transects.

The advantage of the clear 100-m segments is a coarse assessment of prey distribution and abundance even when sampling at the jaguar home-range scale. Start points for transects should be selected randomly within sample cells, then the searches should follow landscape features that yield jaguar sign (tracks, scats, scrapes). See Polisar et al. (2014) for a discussion of jaguar sign. Within each 1-km transect, habitat variables and GPS location are recorded at 100-m intervals. As examples, Sunarto et al. (2012) recorded altitude, assigned scores for overall vegetative cover, canopy cover, sub canopy cover, understory cover, and slope, and included assessments of impact or risk of logging, encroachment, fire, settlement, and hunting at the start of each 100-m section. Because the latter 4 categorical assignments might be subjective, and risk observer bias, they should be complemented by GIS-based assessments of distance from roads, distance from communities, distance from agricultural fields, and distance to discernible water, all feasibly linked to start points of 100-m segments, if GPS locations are recorded faithfully in the field. Recording prey sign along the 100-m segments (Karanth et al. 2011a) will allow a resource-based assessment of habitat quality and threats.

Conclusion

Assessing occupancy of jaguars across the core areas of the NRU will be a challenging project that requires thorough planning. This survey protocol, in combination with general background on occupancy modeling, should provide practitioners with a toolkit to plan such a project. Considering the scope of such a study, we stress the usefulness of collecting pilot data, either in the field or by assembling data from existing studies, to refine and further assess the outlined study design.

Ideally, an occupancy-modeling-based evaluation of the status of the jaguar across the NRU will be complemented by more intensive assessments of abundance, demographics, and population genetics. The extensive camera-trapping surveys we propose to assess jaguar occupancy will allow the identification of focal areas for more intensive studies of jaguar population abundance

and/or density. Areas where jaguars are detected by this large-scale effort can be surveyed with scat-detection dogs (or scat dogs) for genetic analyses; can be targeted with more intensive camera-trap surveys to estimate jaguar population size and demographic parameters using capture-recapture models; and can be foci for capture and collaring efforts to understand jaguar space use, ranging behavior, and social behavior. In these focal areas, the coarse evaluations of prey abundance obtained through occupancy methods can be refined by more rigorous methods, such as distance sampling (Buckland et al. 2008) or fine-grained, prey-focused occupancy sampling (Gopaldaswamy et al. 2012). As such, the outlined occupancy survey will provide the necessary knowledge base to target further conservation-oriented research on jaguars and their prey in the NRU.

ABUNDANCE AND DENSITY

While presence and distribution of species are important state variables that are highly informative and can be reliably estimated through occupancy analyses (see [Occupancy Protocol](#)), it also is important to determine abundance and/or density. Abundance is another way to describe the state or status of a target species, and when converted to density, can be extrapolated to larger areas of similar habitat, potentially to better inform management about a species' overall status. In addition, monitoring abundance through time can tell us whether populations are increasing, decreasing, or remaining stable, giving us insight into whether management actions designed to reverse downward population trends are needed.

Abundance estimation refers to the counting of individuals using a sampling scheme appropriate for the target species, while accounting for imperfect detection, often through a capture-recapture framework. This should be contrasted with a descriptive summary variable such as a trapping rate or capture frequency (i.e., number of captures per some unit of time) because even though trapping rate has been found in some studies to correlate with abundance (O'Brien 2011), other studies have not found such a correlation (Maffei et al. 2011a). Therefore, using a trapping rate as an index of abundance remains controversial (Carbone et al. 2001, Jennelle et al. 2002). However, descriptive variables such as trapping rates can be easily calculated and can give very useful information on hotspots of animal activity or aid in comparing effort and success across studies. But, unless trapping rates have been independently calibrated to abundance, they should not be used as a surrogate for abundance because they do not account for imperfect detection or that the probability of observing a species (or an individual of a given species) is unlikely to remain constant across space and time (Link and Sauer 1998, Pollock et al. 2002). Failure to account for imperfect detection can lead to biased results. Analytical approaches to account for imperfect detection in abundance estimation through capture-recapture analyses are well developed and, below, we describe useful approaches for jaguar abundance/density estimation.

Occupancy analysis refers to the detection of a *species* during repeated visits to a particular site, whereas capture-recapture refers to detection of distinct *individuals* of the target species during repeated surveys at a site. We use the term capture-recapture rather than capture-mark-recapture or mark-recapture, because, in our case, jaguars are already distinctly marked and our proposed methods do not require us to physically mark the individual animals. To conduct a capture-recapture study, we must be able to "capture" unique individuals and "recapture" them later in order to build capture histories for each individual in the population. In our case, the "captures" do not entail physically capturing the animal, but rather we can capture and recapture them noninvasively through remote camera photographs or through DNA from field collected scat (fecal) samples (see also Kelly et al. 2012). The resulting capture histories are used to determine detectability (and what influences detectability) across the population.

In traditional capture-recapture models, detections are recorded in an individual-by-occasion data matrix (the capture history) with entries of "1" meaning the individual was detected, and "0" that

the individual was not detected, during each sampling occasion. The repeat surveys/occasions are needed to inform the detectability model component and ultimately give insight into how many individuals may have been missed entirely (never detected) during the survey. In the more recent spatial (or spatially explicit) capture-recapture framework (e.g., Efford 2004, Royle et al. 2014), the location of capture is also recorded, resulting in an individual-by-trap-by-occasion data array. Detections are not required to be binary, but can instead be counts (i.e., the number of detections of an individual at a given trap in a given occasion). This is particularly useful in camera-trap studies, where data are not limited to “detected or not” (as opposed to, for example, hair snare studies, where we can only determine whether or not an individual has visited a trap during an occasion or not).

Factors that are known to impact detectability and thus the resulting abundance estimates, and that are commonly included in capture-recapture models, are: time $M(t)$ variation related to survey-specific details such as good or bad weather during surveys; behavioral variation $M(b)$ due to a trap response such as trap happiness or trap shyness; individual variability or heterogeneity $M(h)$, which can result from unobserved sources, or be caused by differences between males and females or young and old animals; and combinations of these factors. Spatially explicit capture-recapture (SCR) models further allow us to model trap-level effects on detectability. For large cats, for example, camera traps set up along small, dirt roads often have much higher detection rates than cameras set off of roads (Conde et al. 2010, Harmsen et al. 2010, Sollmann et al. 2011).

Like occupancy modeling, there is a large range of capture-recapture models and the most relevant to this protocol are discussed briefly in the section [Types of Abundance/Density Models](#). The simplest model is the “closed-capture” or “closed-population” model, which is analogous to the single-season occupancy model. In this case, we assume that abundance is constant during the survey period such that there are no births/deaths (demographic closure) and no immigration/emigration (geographic closure). Detectability is allowed to vary according to factors listed above. The closed-capture model can be extended to an “open-population” or “robust-design” model, analogous to the multi-season model in occupancy. This allows us to determine what drives changes in population abundance (e.g., survival and recruitment) from data collected over a longer time frame, such as multiple years.

The following protocol focuses on the design of closed-capture surveys for jaguar abundance estimation in targeted core areas of the NRU. We suggest 2 ways to do this through remote camera capture-recapture, and through genetic capture-recapture. We give suggestions regarding practical aspects of capture-recapture (hereafter often denoted CR) modeling along with jaguar-specific CR suggestions for the NRU. We also suggest extending the closed-capture protocol to conduct open-population, robust-design modelling using remote camera data only. Finally, we suggest analytical methods to address jaguar prey abundance and sympatric predator abundance, which can be determined from the non-target data collected via remote camera traps set for jaguars.

Practical Considerations

Definition of occasion—As with occupancy estimation, determining detection probability (in this case for individual jaguars) requires repeat surveys of the target area. Surveys can be conducted by using remotely-triggered infrared cameras to “capture” images of jaguars, which have natural markings on their coats that allow identification of individuals by their distinctly different rosette patterns (Silver et al. 2004). Traditionally, repeat surveys are achieved by surveying the study area over multiple temporal occasions. Camera “traps” are operational continuously throughout the designated survey time. While it would seem reasonable to use a 24-hour time period as a repeat survey occasion, this often results in an overload of zeroes in the data set because cameras may go many days or weeks without photographing a jaguar, which can lead to computational problems caused by detection being close to zero. Therefore, most jaguar studies “collapse” data into somewhat arbitrary time periods such as 3, 5, or 7 (sometimes up to 14 days; Noss et al. 2013). However, if occasions are too long, loss of information important to determining detectability can occur because an animal captured 3 days in a row would only be counted as detected once in a 3-day, collapsed data set (Polisar et al. 2014). There is a trade-off between computational problems caused by too many zeroes in the data set, and loss of information on individual detectability when collapsing data into multi-day occasions. Seven days (1 week) may be an appropriate time period for data collapsing for abundance estimation in the NRU, but this length of time can be decided upon after exploratory analysis performed on data in hand to determine appropriate occasion length. For genetic capture-recapture, surveys can be conducted by searching the study site and “capturing” animals through collecting their scats and determining both the species and the individual through DNA analysis (i.e., molecular scatology; Kohn et al. 1995). There are 2 approaches for determining occasions. Researchers can search an entire study site for a predetermined number of kilometers over a predetermined number of days (considered 1 encounter/capture occasion), and then repeat the search (i.e., temporal replicates) of the full study site up to 4 or 5 times to create 4 or 5 encounter occasions (Wultsch 2013). Alternatively, researchers can search a study site only once, but use spatial replicates – usually distinct trails or predetermined grid cells. These spatial replicates can be used as repeated encounter occasions. While this may be more efficient and quicker, it precludes the analysis of time $M(t)$ models, as spatial replicates cannot be all surveyed at the same time (i.e., there are no temporal replicates). Additionally, the spatial replicate design may not yield a high enough number of captures and recaptures to estimate abundance in an area such as the NRU with low jaguar densities.

In theory, spatial capture-recapture models do not require temporal repeats to estimate detection probability, because they make use of the spatial information in the data (Borchers and Efford 2008). In practice, however, we are unlikely to ever collect enough data on a single sampling occasion to obtain reliable density estimates. But even when an area is surveyed for several weeks or months, there is no need to subdivide the survey into discrete occasions (e.g., Borchers et al. 2014), unless temporal variation in detectability is to be modeled. In the special case of

camera traps, the sum of records of each individual at each trap can be used as input data. This has the great advantage, especially for rare species, that we do not lose information by condensing data into a 0/1 format. Borchers et al. (2014) show that using all records does lead to more accurate and less biased parameter estimates. It is important to note, however, that records are assumed to be independent. As a result, some sort of threshold should be established for what constituted independent records of the same individual at the same camera trap (e.g., at least an hour between subsequent records, or 1 day). While Polisar et al. (2014) cite the threshold of 0.5 hours that O'Brien (2003) also followed in Kinnaird and O'Brien (2012) for considering consecutive photographs of the same individuals independent for relative abundance indices, a suitable range of thresholds for jaguars in the context of spatial capture-recapture input has yet to be established.

Definition of sampling units—When estimating abundance, the individuals detected are the sampling units, in contrast to occupancy, where the sites surveyed are the sampling units. For abundance, the number of times jaguars are recaptured also determines whether the sample size is large or small. There is no set number of sampling units (jaguars) needed for sampling, but a sample of 30 or more individuals will yield more precise estimates (Tobler and Powell 2013). Unfortunately, jaguars exist at such low density that most jaguar camera-trapping studies do not reach 30 individuals sampled despite large amounts of effort. In Sonora, 1,560 trap-nights in a relatively small area yielded 4 individual jaguars (Rosas-Rosas and Bender 2012), and 7,718 trap-nights in an area of variable size in another area yielded ten individual jaguars (Gutiérrez-González et al. 2012). Moreno et al. (2013) reported 11 jaguars from 8,408 camera trap days across an area whose total dimensions were estimated at 408 km², with samples drawn for 2.5 years. In Chamela-Cuixmala in Jalisco, 725 trap-nights photographed 8 individual jaguars (Núñez-Pérez 2011). Because jaguars use large spaces, the “net” of camera trap stations needs to be large to sample a substantial proportion of the population, and for analytical models to function well. Therefore, in general, we suggest aiming for large trapping grids to increase the potential to capture more individuals (Maffei and Noss 2008, Maffei et al. 2011a, b, Noss et al. 2013, Tobler and Powell 2013).

Sample size, survey area size, camera spacing, and allocation of effort—In occupancy analysis, sample size has 2 components that are the number of sites surveyed and the number of repeat surveys at each site, both of which can be defined/controlled by the researcher. In abundance estimation, however, we can only control the number of detectors (e.g., camera traps) and of repeat surveys, and must “guesstimate” (or conduct a pilot study) how much area needs to be surveyed in order to obtain enough distinct individuals, and recaptures of those individuals, to obtain accurate and precise abundance estimates. The area covered in camera-trapping surveys is determined by a combination of how many traps are used and how far apart we place those traps on the landscape. Traditional CR models required that spacing between traps should be such that individuals with the smallest recorded home ranges (usually females) would not be missed by putting camera traps too far apart. For example, camera spacing for jaguars in Belize is often 3

km based on the smallest home range recorded for 1 female radio-collared jaguar of 10 km² (Rabinowitz and Nottingham 1986). This ensures every 9 km² will contain a camera trap; hence, no individual jaguar should be missed due to holes in the trapping grid. This ensures that every animal has a probability of being captured, a necessary assumption of CR models (Otis 1978). With spatial capture-recapture models, this is no longer required. Still, because we require that individuals are recaptured at multiple sites, it is advisable that, on average, camera traps are spaced narrower than animal movements. But “holes” in the trapping grid that are large enough to contain an entire animal’s home range do not constitute an assumption violation to spatial CR models. This allows for much more flexibility in spatial study design. For example, for surveys of large areas, it is possible to distribute multiple clusters across a landscape, where narrow spacing within a cluster allows recaptures of individuals at multiple traps, whereas the wider spacing among clusters allows exposing more individuals to the survey (Efford and Fewster 2013, Sun et al. 2014). Careful consideration should go into spatial study design and we suggest conducting simulation studies under several sampling scenarios to determine whether a design is adequate for the study area (Sollmann et al. 2012*b*, Efford and Fewster 2013, Tobler and Powell 2013, Sun et al. 2014).

As for spatial extent of the survey, the larger the area covered, the more individuals will be captured, thus increasing sample size. Original recommendations were to cover an area using at least 20 camera stations that encompassed 3 to 4 times the average home-range size (Maffei and Noss 2008). These recommendations have recently given way to a newer, more convincing study by Tobler and Powell (2013) showing that even twenty stations might be inadequately small and that increased area and camera numbers are needed to improve accuracy and precision of density estimates (see [Trap Distance, Camera Numbers, and Spatial Extent](#)).

The duration of the study should be such that it satisfies the assumption of population closure while still acquiring enough captures and recaptures to enable (spatial) CR modeling. For demographic closure, this can be done by keeping the duration of the survey short (on the order of 2 to 3 months) relative to lifespan of the animal.

For conducting genetic capture-recapture, the sample size is going to be based on the number of individual jaguars captured and recaptured, not simply the number of scat samples collected. An additional complication is that not all the samples will amplify, meaning that we will not be able to obtain DNA from every scat sample. Some information will be lost, similar to the lost information from unidentifiable, blurry photographs. Therefore, we suggest intensively searching for scat samples across the same large area where camera traps are deployed to potentially encounter more individuals. It is likely that temporal replication will be needed (see [Definition of Occasion](#)) to obtain enough scat samples (specifically recaptures) to conduct genetic capture-recapture. Temporal replication can easily be done within the same amount of time that remote cameras are deployed (3 months), thus satisfying population closure for genetic sampling.

Survey Protocol for Monitoring Jaguar Abundance and Density

The following survey protocol aims to evaluate and monitor jaguar abundance and density across the core areas of the NRU over fifteen years. Jaguar cubs remain with their mothers for 1.5 to 2 years (Seymour 1989). Female jaguars become reproductively mature at 2-3 years (Seymour 1989). Few jaguars live beyond 12-13 years (U.S. Fish and Wildlife Service 2012). A 5-year period spans the maturation of female jaguars, and the maturation of at least some of their female offspring. Because 5 years constitutes a generation, it is a reasonable and cost-effective interval to measure numerical population trends (increasing, decreasing, stable). Fifteen years includes 3 generations, and thus, is a good benchmark to assess progress towards recovery goals.

We focus on closed-capture modeling for a single season but also provide guidance on extending surveys over multiple seasons in order to detect changes in population abundance through time. Our recommendations are based on jaguar ecology, experience of the authors with jaguar-specific surveys and the logistical constraints of the NRU, and our experience with analytical methods for abundance and density estimation from remote camera or genetic capture-recapture surveys. The following study design touches on these issues and can be refined based on review of pilot study data from suggested target areas.

Abundance/Density Estimation Field Techniques

There is now a relatively long history of using remotely triggered camera traps combined with (spatial) CR modeling for estimating abundance and density of large wild cats, beginning with tigers in the mid-1990s (Karanth 1995, Karanth and Nichols 1998). The first studies using remote cameras for jaguars followed nearly 10 years later (Kelly 2003, Wallace et al. 2003, Silver et al. 2004). More recently, advances in genetic techniques, specifically molecular scatology (see [Population Genetics](#)), have opened the door to estimating abundance through combining genetics with CR techniques for large cats (Mondol et al. 2009, Naidu et al. 2011, Gopalaswamy et al. 2012b, Wulsch 2013). Below we suggest a protocol for using remote camera CR and genetic CR for estimating jaguar abundance and density.

Choosing Sampling Sites

For abundance estimation, it is most efficient to choose an area where a known jaguar population exists, and intensively study that area with systematically-spaced camera traps or scat surveys. While other areas of low population density might be of interest ecologically, the amount of effort needed to accumulate a sufficient sample size is likely prohibitive. In the NRU, data describing breeding populations comes from the Sahuaripa-Huasabas area in northern Sonora and in Chamela-Cuixmala in Jalisco (Núñez-Pérez 2006, 2011, Gutiérrez-González et al. 2012, Rosas-Rosas and Bender 2012). Additional information suggesting intact populations is being collected from Cabo-Corrientes along the Northern Jalisco Coast, RBSM straddling Jalisco and Colima, and RBMNN (wetlands) and Sierra de Vallejo in Nayarit (Núñez and Vazquez 2013; Núñez in prep).

Jaguar populations are also being monitored in the APFF Álamos-Río Cuchujaqui (Gutiérrez-González et al. 2013).

In the mega-landscape monitoring scenario we recommend, occupancy surveys are used to evaluate a large matrix where jaguars may or may not occur to discern distribution and occupancy trends. The occupancy probabilities and detection rates will identify core areas where jaguar populations are concentrated, as well as clarify the environmental and management covariates associated with jaguar distribution. Focused studies of abundance, as well as demographic and dispersal characteristics, can increase our understanding of the factors that influence jaguar distribution in the larger matrix, and are essential for recovery. Due to the labor and expense involved in more intensive studies, these focal areas for long-term research need to be selected carefully. While occupancy evaluates where jaguars are, an essential metric for recovery, more intensive studies in focal sites evaluate the dynamics that drive that distribution.

Trap Distance, Camera Numbers, and Spatial Extent

In the Chamela-Cuixmala Biosphere Reserve in Jalisco, Núñez (2006) recorded average female home ranges of 23.8 km² in the dry season, and 38 km² in the wet season. Using 25 km² as an approximation of the smallest female jaguar in the NRU, we suggest systematic camera station placement at 4-km intervals. This will ensure that every 16-km² block contains a camera station and therefore each individual should have a probability of being detected by a camera, and most individuals should be exposed to several cameras. Camera station placement across the landscape can be done in 2 ways. A grid of 4 km x 4 km blocks can be overlaid across the area of interest and 1 camera station placed in each block in the best possible location that increases probability of capture (e.g., on known travel paths of jaguars such as roads, trails, junctions, water holes). Another approach is to set cameras at regular intervals such that each station is 4 km (± 200 m) from at least 2 other stations, except for cameras on the outer edge that may be 4 km from only 1 other station (a technique used for jaguars in Belize; Marcella Kelly, Virginia Polytechnic Institute and State University, personal communication).

Recent work by Tobler and Powell (2013) offers new guidance on camera numbers and size of the camera grid needed to deliver robust estimates of abundance and density. They reviewed over 74 studies and showed that 90% produced biased results that overestimated jaguar density, largely due to covering too small of an area. This overestimation is in large part an artifact of using non-spatial CR models, where abundance is converted to density in an ad hoc manner, using information on how far individuals moved among traps. These “movement estimates,” used to derive an effective sampled area, are limited by the extent of the trap array and heavily influenced by trap spacing (Maffei et al. 2011*a, b*). Spatial CR models have largely overcome these problems by integrating the spatial information of capture (Noss et al. 2013, Tobler and Powell 2013). Therefore, spatial CR models are much more robust to spatial study design than traditional CR models (e.g., Sollmann et al. 2012*b*). Overestimation would be a serious problem for conservation of jaguars in the NRU and we do not want to obtain flawed, overly optimistic

estimates for an endangered species. Simulations showed that as camera grid size approached the size of 1 home range, precision increased rapidly and that the maximum camera spacing that still gave accurate results was about half a home-range diameter (Tobler and Powell 2013). The radius and diameter of home ranges from 25-200 km² are provided in Noss et al. (2013). Our suggested camera spacing of 4 km is larger than the suggested spacing of half a home-range diameter for females, which would be 2.8 km for a 25 km² home range in Jalisco. However, this value represents the minimum home-range size, and we assume that male home ranges in the NRU can be as large as 500 km². Therefore, this spacing is a compromise between these disparate home-range sizes and the need for large spatial coverage.

Spatial extent of the camera grid depends somewhat on jaguar density. Areas with high jaguar density (>3 per 100 km²) might only need to be as large as half to 1 jaguar home-range size, while areas with low jaguar density (< 1 per 100 km²), as in the NRU, will need to cover more than 1 jaguar home-range size to produce accurate and precise estimates (Tobler and Powell 2013). We suggest using a minimum of 60 camera-trapping stations, which is in line with suggestions by Tobler and Powell (2013) to use 60-100. This number will be necessary due to the low jaguar density and large home ranges for males in the NRU. Using 60 camera stations at 4-km intervals will result in a camera grid size of ~960 km², or about 2 of the largest jaguar home ranges noted for males. This size also is equivalent to nearly 2 hexagons from the [Occupancy Protocol](#) and is in line with Tobler and Powell's (2013) recommendation to cover 500-1,000 km².

Genetic Sampling for Abundance and Density

We suggest conducting genetic sampling within the same ~960 km² areas delineated by the camera trapping grid as this will enable comparison of the effectiveness of the 2 different methods, allow for combination of the 2 methods to improve density estimates (Gopalaswamy et al. 2012b), and give detailed genetic information from the focal areas of the NRU. Additionally, efficiency can be increased by placing at least 1 hexagon from the [Occupancy Protocol](#) within each of these 4 focal areas and using the scat data collected for both occupancy and abundance/density.

We suggest using temporal replicates, rather than spatial replicates, in order to increase sample sizes of captures and, especially, recaptures needed for CR analyses. For flexibility in searching, a 4 km x 4 km grid (16-km² grid cells) can be superimposed across each study site and each 16-km² grid cell opportunistically searched for approximately 8-10 linear km along established roads, trails, game trails, and other likely travel paths, following the techniques described in Wulsch (2013). In this type of opportunistic searching, the researcher should use these likely carnivore paths in order to increase detections of scat samples, as carnivores are known to mark on paths and at prominent locations including road junctions, for example. A distance of 8-10 km searched per grid cell enables researchers to standardize effort across grid cells, but allows flexibility in choosing the search paths through the grid cells. The 8-10 km searched should be

along paths within each grid cell. Completion of all cells in the survey will constitute 1 sampling occasion. The survey will then start over searching all cells again, until 4 to 5 repetitions have been completed. It should be noted that the same trails can be surveyed, or different trails can be searched with each repeat survey to cover more spatial area within each grid cell.

Sampling Duration

Camera trapping—With rare and elusive species, researchers usually need to compromise between sampling long enough to collect enough data, but short enough so that the parameter under investigation is biologically and ecologically meaningful. Closed-capture models require that no individuals in the study population die or emigrate, and that no new individuals are recruited, over the course of the survey. Approximating this assumption is usually done by keeping surveys relatively short. The amount of time depends on the biology of target species and, for big cats, a study duration of 2 to 3 months is generally adequate (Henschel and Ray 2003, Silver 2004). This usually enables enough captures and recaptures to run CR analyses while meeting the demographic closure assumption. Demographic closure also can be evaluated through closure tests (Otis 1978, Stanley and Burnham 1999). In practice, it can be difficult to distinguish between lack of population closure and heterogeneity in detection. Jaguars not recaptured may have emigrated, or died, or may have simply eluded re-detection as the study progressed. New animals might be immigrants, or their movements may not have initially coincided with the location of camera trap stations. Using simulations, Tobler and Powell (2013) found that short periods reduced precision and confidence intervals. They recommended minimum periods of 60 days, and even sampling durations of 90 or 120 days, stating that in most situations the data gained by extending the survey period should outweigh the risk of violating closure. Geographic closure (i.e., no immigration or emigration) is a harder assumption to meet over a 3-month trapping period, because some sampled individuals may permanently move, or may have home ranges that extend beyond the edges of the sampling grid, thus temporally emigrating from the grid. Geographic closure can be assessed using the Pradel model (Pradel 1996) implemented in program MARK. Every month of an extremely large camera-trapping survey is expensive. Thus, the minimum number of days required to level out density estimates and coefficients of variation becomes as important for the budget as it is for the science. For example, simulations predicted the need for a sampling duration of over 90 days in a jaguar camera-trapping study in Guatemala. However, preliminary results from this study show a steep curve of new individuals lasting up to approximately 70 days, with no appreciable changes in density estimates after 60 days. Additionally, steep declines in the coefficients of variation with increasing study duration level out at approximately 60 days and become gradual thereafter. The preliminary results of the large scale test of the simulations in Tobler and Powell (2013) suggest that 60 days were adequate for accurate results, and that extra time yielded diminishing returns despite added expenses (Rony Garcia, Wildlife Conservation Society, personal communication).

Unlike the [Occupancy Protocol](#), where surveying such a large number of 500 km² hexagons will take many months, setting up camera for the intensive abundance surveys should each take about

2 weeks and then run continuously for 3 months. This is reasonable considering that camera stations are spread continuously in relatively close proximity across the grid.

We also suggest sampling during the dry season to avoid camera trap malfunctions due to high moisture and logistical complications in reaching the field sites during the wet season. In Jalisco, the dry season lasts from October to May, in Sonora from November to June. This also may be more appropriate for the closed-capture models if jaguars change their ranging behavior as seasons change, potentially violating geographic closure.

Genetic sampling—Genetic sampling can take place entirely within the 3-month sampling period when cameras are functional. The amount of time it will take for each repeated scat survey (i.e., each encounter occasion) across the entire study site will depend on how many, and what type of, searches are used. To increase efficiency of finding scat samples, we recommend using scat-detection dogs rather than people searching for scat visually. Scat-detection dogs have been shown to be highly efficient in finding jaguar scats in other studies (Vynne et al. 2011, Wultsch 2013, Wultsch et al. 2014). We suggest using 2 scat-detection dog teams to complete surveying such large areas repeatedly in 3 months. Each dog team could search nearly 2 of the 16-km² superimposed grid cells per day. With 60 grid cells, that would take about 15 days per occasion plus several days rest for approximately 20 days per occasion. With this schedule it would be possible to complete 4 (possibly 5) repetitions in 90 days. It is likely that 10-12 scats per 15-day occasion could be collected, and up to 50 scats after 4-5 repetitions.

Setting and Checking Cameras

The main difference between camera sets for occupancy versus abundance is the requirement of having 2 cameras per station for abundance estimation, rather than 1 (see [Figure 7-8](#)). Cameras are set on opposing sides of the target area to photograph both flanks of the jaguar for individual identification based on unique spot patterns. Cameras should be at least slightly offset to prevent mutual flash interference; however, some researchers prefer to have the opposing cameras within each camera's viewshed to record interesting behaviors, such as when animals investigate the opposing camera. This can also lead to multiple photos of individuals, aiding in individual identification. Additionally, cameras should be set to take multiple photos (at least 3) with each triggering event to improve identification success. Wait time between triggering events should be short (15-30 seconds), because some studies have noted cats following each other in either family groups or male/female pairs (Marcella Kelly, Virginia Polytechnic Institute and State University, personal communication).

Camera station locations can be decided based on past experience of jaguar researchers in the target areas and through GIS mapping of locations based on spacing requirements suggested above. In the field, however, cameras should always be placed to maximize capture probability by using established trails, dirt roads, canyons, ridgelines, water holes, river edges, or other features that jaguars are known to use and which funnel animals in front of the cameras

(Harmsen et al. 2010, Sollmann et al. 2011). Randomly placed cameras usually have very low jaguar detection and will not generate enough data for CR modeling. More detailed and specific information regarding camera placement can be found in the [Setting Cameras](#) subsection of the Occupancy Protocol and we refer to this subsection for suggestions on camera setting in the field.

We suggest having a “camera setup data sheet” that includes documentation of local conditions at the site such as: trail or road type (e.g., game trail versus human trail, or logging road versus 2-track), trail or road width, canopy cover, habitat type, presence of water, land use category, etc. ([Appendix 6](#)). These data may clarify variables important to study animals. Apps et al. (2006) used data from 30 independent variables in a 5,496 km² systematic DNA hair-trap survey to describe interspecific landscape partitioning between grizzly and black bears according to terrain, vegetation, and land cover variables at 2 separate scales. We also suggest checking cameras periodically to troubleshoot malfunctions, and change batteries and memory cards as necessary ([Appendix 7](#)). The amount of time between camera checks depends on local weather conditions and logistics. In wetter areas, more frequent checks will be needed, as humidity is known to negatively affect camera functionality. Some tropical studies check cameras every ten days (Marcella Kelly, Virginia Polytechnic Institute and State University, personal communication), while in dryer areas this could be lengthened. We suggest triggering each camera at setup, at each camera check, and at retrieval, with a trigger card displaying the date, station code, camera number, and time, as this information can not only aid in data organization, but also in correcting photo data if the camera’s date/time stamp malfunctions. We suggest using a “camera checking data sheet” to record all relevant information (e.g., battery levels, camera condition, number of triggers) at each camera check. Example data sheets can be found in Sunarto et al. (2013) and an example is provided in [Appendix 8](#).

Setting and checking of camera traps also provide for opportunistic collection of jaguar scats (see [Opportunistic Searches](#) and [Scat Collection](#)). Scat and other opportunistically-collected data (e.g., tracks, skins) should be recorded in the jaguar observation database (see [Data Capture and Curation](#)).

Surveying with Scat-Detection Dogs

Details and specific information regarding training and survey with scat-detection dogs can be found in the [Sampling Using Scat-Detection Dogs](#) subsection of the Population Genetics discussion, below.

Data Recording

Photographic records—As with occupancy analysis, all photographic records should be entered into a comprehensive database with a single record for every independent photographic event, including humans and domestic animals. A single photographic event is often recorded as any distinctly different individual within a 30-minute time period regardless of the number of

photographs of that individual (Davis et al. 2011). From there, it is relatively easy to manipulate the raw data in order to calculate trapping rates for all species, to create detection/non-detection matrices for all species, and to create capture histories for individual jaguars. Similar to occupancy, information associated with each record should include, at minimum: species common and scientific names, individual ID for jaguars, sex and age if possible, number of individuals in the picture, total number of photographs of each event, time of day, date, camera-trap station identifier and/or coordinates, camera(s) that triggered, study site, and survey identifier (if multiple surveys are run in a study site).

The main difference between occupancy and abundance in camera-trap data entry is that for abundance there are 2 cameras per station instead of 1. This complicates data entry because 2 cameras can photograph the same animal and these should not be double-counted as 2 separate photographic events – they are the same event, but with 2 photographs. Therefore, researchers must simultaneously examine data from both opposing cameras and determine if the events are the same or different. The camera's date and time stamp aids tremendously, unless it malfunctions, in which case deciphering independent events can be a somewhat onerous task. Attaching a laptop or desktop computer to a separate monitor (or 2) can ease data entry by keeping separate cameras at the same station each on a different monitor while conducting data entry. More details on data entry from camera traps can be found in Sunarto et al. (2013). Examples of jaguar capture histories are provided in [Appendix 9](#).

As with occupancy, it is essential to store photographs in a manner that makes locating a specific record easy, e.g., in a folder structure that identifies the survey site, camera trap site, the camera number, and date range. Because abundance studies have 2 cameras per station, it will be necessary to uniquely label each of the 2 cameras at each station. It is helpful if this identifier includes the camera model such as RX01 (for Reconyx 01), or some similar naming pattern. This is especially helpful when using more than one camera brand and model. Specific software is available to store camera-trap data and link spreadsheet records to photographs and we refer to the [Occupancy Protocol](#) for a description of platforms such as Camera Base, DeskTEAM, and ExifPro.

Regardless of the chosen platform to manage and archive data, we provide a standardized spreadsheet for jaguar detections in [Figure 9](#). This spreadsheet is designed for compatibility with the Jaguar Event-Record Database (<http://jaguardata.info/>) developed by WCS. The necessary user interface for easy batch import of jaguar observations from camera-trap data (and other data sources) using this standard spreadsheet could be developed to increase the time and efficiency with which large datasets from camera trapping or telemetry could be incorporated with the existing database. Importing jaguar observations into this overall presence database will help centralize information on jaguar occurrence and allow researchers to find out about jaguar studies throughout the species' range.

Scat collection and recording—See [Population Genetics](#) section for details regarding how to handle and collect scat samples for genetic analysis. In addition, a data sheet will be needed that records date, time, GPS location of each scat sample, local conditions (e.g., trail type, weather, scat condition). Additionally, it will be necessary to record all paths traveled, preferably downloaded from the recorded tracks of a hand held GPS unit. These will be needed later to assess effort in each grid cell, and can aid in determining how to assign scat locations to stationary detectors for spatially explicit capture-recapture modeling (see [Types of Abundance/Density Models](#)).

Survey information—It is important to keep track of survey related information, such as camera-trap location (X and Y coordinates), date of installation, date(s) of checking, date of final retrieval, and local characteristics of camera setup (see [Setting and Checking Cameras](#) for suggestions on “camera setup data sheet” and “camera checking data sheet”). If upon checking or retrieving, a camera unit is not working (because it is malfunctioning, out of battery, or out of storage space), this should be recorded. Extra cameras should always be brought into the field to immediately replace ones that are not functioning. It is very helpful to take test pictures using a trigger card that has the station code, date, time, and the camera unit (especially when you have 2 cameras per stations). This aids in keeping track of camera functioning and in organizing and labeling large numbers of folders of camera trap data. This also allows for easy calculations of survey effort, such as number of functioning trap-nights at each station and across all stations for the entire survey. Writing the time and date on trigger cards enables researchers to back-calculate correct dates and times of photographs when/if the camera displays incorrect dates/times due to malfunctions.

Data also should be entered with a single line for each camera station (regardless of if there are 1 or 2 cameras) and a column for each day of the survey, from the day the first camera was set up to the day the last camera was removed, with entries of “0” or “1,” depending on whether a given camera trap was installed and functioning on any given day (1) or not (0). These data are necessary for spatially-explicit density estimation, which requires information on whether a particular station was available for trapping animals. When using 2 cameras per station, the station is generally still considered as functioning as long as 1 of the 2 cameras is operational.

For genetic sampling, it is important to make sure that scats collected in the field are easily matched to data sheets and later genetic samples. Refer to [Population Genetics](#) section for more information.

Covariates—Detection can be modeled as a function of covariates, and most modeling platforms already include the common influences on detectability: time effects, behavior effects, individual heterogeneity, and combinations of these effects. Other covariates that have been shown to improve abundance/density estimates are sex of the animal (males usually have higher detectability than females) and camera or scat sample location (road stations usually have higher detection rates than off road stations) (Sollmann et al. 2011, Wultsch 2013). Unlike occupancy,

where landscape covariates can be extracted from a GIS database from multiple survey cells (n=133 in our [Occupancy Protocol](#)) and used to predict occupancy in cells not surveyed (see also Sunarto et al. 2012), this is not usually done in an abundance context because the scale of abundance surveys is much smaller and the outcome is a single abundance/density estimate for only a single area. We do propose, however, to survey 4 areas for abundance, and this may give us some insight into how abundance or density varies across the landscape. Detection also can be modeled as a function of location-specific covariates, such as habitat variables collected surrounding each camera trap or scat sample, but modeling from here would be only within-grid modeling of either trapping rates (Davis et al. 2011) or within-grid occupancy analyses (Sunarto et al. 2012), which would be equivalent to modeling animal activity or habitat use within a grid, rather than true occupancy. See [Setting and Checking Cameras](#) for examples of site specific covariates for camera traps, or review Davis et al. (2011) and Sunarto et al. (2012) for micro-habitat features to measure surrounding camera traps. Micro-habitat sampling surrounding scat samples can follow similar protocols as surrounding camera traps, but other variables related to scat condition could be useful (e.g., substrate, scat color, moisture content, presence of mold), especially because these can also be linked to DNA amplification success.

Abundance/Density model input and data format—Structure of the input files varies depending on the software used for implementing abundance/density models, but all software programs require an individual-by-occasion, detection/non-detection matrix, and this may allow the covariate of sex depending on software. Other input files include a list of station identifiers and their GPS locations, a site-by-individual matrix (list of locations where individuals were captured), a site-by-occasion matrix depicting when (and where) cameras were operational or the site was searched for scats, and a file depicting the locations of hypothetical home-range centers. These hypothetical home-range centers should be spaced at regular intervals across the landscape, the closer the better, with an understanding that computing time will be longer with more home-range centers. Input may include site-specific habitat covariates.

Data Analysis

Many platforms exist for abundance/density analyses. We have divided these up into: 1) traditional approaches, and 2) SCR approaches for clarity. We strongly recommend the use of SCR approaches, because these represent a major improvement over traditional approaches, especially for species like the jaguar that occurs at low densities and moves over large areas.

Traditional model platforms include Programs CAPTURE (frequentist approach; Otis et al. 1978, Rexstad and Burnham 1991) and MARK (information theoretic approach; White and Burnham 1999), both of which estimate abundance only and the user must determine the area surveyed in a separate analysis to use in converting to density. Spatially explicit modelling platforms include Program DENSITY or the equivalent R package secr (information theoretic approach, Efford 2004, 2011, Borchers and Efford 2008), and program SPACECAP implemented in R (Bayesian approach; Singh et al 2010, Gopaldaswamy et al. 2011), which

incorporate the spatial locations of the camera traps or scats detected directly into the modeling process and estimate density directly. Implementing density models in a Bayesian framework also is fairly straightforward using programs such as WinBUGS (Gilks et al. 1994) or JAGS (Plummer 2003) and offers more flexibility in model building or incorporating covariates. For a discussion of abundance/density models, see [Capture-Recapture Modelling for Abundance and Density](#).

Equipment and Costs

Personnel—Field work should always be conducted in teams of at least 2 people. A field assistant will cost approximately 750 USD per month in salary. As a frame of reference, in a 300-km² survey of Mexican wolves and their prey, 3 teams spent 3 days in the field to set up 30 camera trap stations (Carlos López-González, Northern Rockies Conservation Cooperative, personal communication). This translates to 1 team-day (i.e., 1 team working 1 day) per 3.3 camera traps. Scaled up to the suggested design of double the number of camera stations at 60 stations, each abundance survey would require 18 team-days per survey to set up stations and could be done in 6 days using 3 teams (assuming similar camera spacing).

The costs estimated here do not include time spent determining field locations, including obtaining landowner permissions to access land (if needed), time for programming cameras, field team housing, vehicle purchase or rental, or vehicle running costs. Also, there will likely be substantial person-hours needed for data entry and analysis, which include identifying species and individuals on photographs, transferring photo records into a database, creating capture histories and other files needed for modeling, and modeling itself.

Scat collection personnel —Two dogs and 2 handlers are required. Researchers have the option of either contracting or collaborating with commercial conservation scat-detection dog organizations or training their own dogs and handlers. Commercial conservation dogs average 400 USD per day for a team of dogs, handler, and orienteer, which translates into ~8,000 USD per month. Alternatively, the University of Arizona Jaguar Survey and Monitoring Project purchased a dog and trained the dog and handler using U.S. Border Patrol methods (Melanie Culver, University of Arizona, personal communication). The dog handler is paid 13 USD/hour and the team can work 6 hours/day and 30 hours/week, yielding total wages of 1,500 USD per month plus benefits.

Scat collection equipment—Field equipment requirements are fairly minimal for detection dog work and consist of a handheld GPS unit for each orienteer and a small GPS unit carried in the pack of each working dog to document the search track each day. These GPS units run anywhere from 200-500 USD depending on brand and quality. Generally, handheld GPS units should be of high enough quality to record 8-12 hours of data every 20-30 seconds and have the capability to download resulting tracks into associated programs such that search tracks can be imported into GIS programs. Additionally, detection dog teams will need Ziplock® bags for collecting scats in

the field and centrifuge tubes to transport detected scats in the appropriate storage agent (i.e., either 95% ethanol or buffer agent) to the lab. The detection dog contractor should provide all goods and services required for the completion of the above sampling tasks, which include, but are not limited to: veterinary care, food, water, rewards, GPS units, and batteries. There may be costs associated with obtaining any necessary permits and/or landowner permission for conducting transect sampling with canines in the areas selected. Finally, vehicle operating and maintenance costs will need to be accounted for as well.

Camera traps—Depending on the model, camera traps cost between 250-500 USD (including memory cards, cables, and locks). For each abundance survey, a full study would require approximately 150 cameras, which includes 2 cameras per station for 60 stations (120 cameras) plus an extra 30 cameras to replace malfunctioning, vandalized, or stolen cameras. If executing more than one abundance survey, we suggest running them sequentially. For example, if there were 2 sites in Sonora, once the abundance survey is completed in Sahuaripa-Huasabas, cameras could be moved immediately to Alamos, for a total of 6 months of surveying (3 months in each location). The same schedule could be followed simultaneously in the Jalisco Core Area by moving cameras sequentially between 2 sites. In this way, 150 cameras would be needed for each area (northern and southern) for a total of 300 camera traps total for the 4 survey areas. Depending on the camera model, this would range from 37,500-75,000 USD.

See [Occupancy Protocol](#) for a description of various types and features of remote cameras. However, because abundance estimation requires individual identification, cameras with high resolution are essential for clear images of coat patterns needed for individual identification. This is different from occupancy, which only requires species identification. White flash may also be necessary for clear images at night, but this feature must be balanced with the potential increased risk of theft due to increased conspicuousness. Scent devices can be installed to slow cats down in front of the camera to increase the chance of a high quality, non-blurry pictures. We also suggest setting cameras to take multiple photos at each triggering event to improve success of individual identification (see [Setting and Checking Cameras](#)).

Genetic costs—If we assume that a 15-day session with the scat dog produces 10-12 scat samples, and those sessions are repeated 4 (possibly 5) times, then a total of 40-50 jaguar scat samples will be collected. These samples will need to be genetically analyzed to confirm species ID, then, if identified as a jaguar, a gender identification will need to be performed, followed by individual identification. The cost of species, gender, and individual ID is 100 USD per sample, which includes labor, materials, supplies, and analysis of data. For 50 scat samples per 90 days of searching, the cost is 5,000 USD. Also, if desired and funding is available, diet analysis can be performed on bone and cartilage found inside the scat. Diet involves decalcification of the bone prior to DNA extraction, which is labor intensive, but only species ID on the molecular end is needed, so the cost is 40 USD per bone sample, or a total of 2,000 USD if all the samples were genetically identified as jaguar. Chances are that there would be some dropout for samples that

did not work or are not jaguar, so this cost is more likely to be around 1,000 USD for the 90 day period. This includes 1 bone sample per scat.

Other—The initial investment that 16-GB memory cards represent will pay for itself in the guarantee of no lost data, and potentially less labor to check units. Theft-proof metal boxes that can be bolted and/or locked to a tree or post are available for many camera brands and these should be considered in areas with theft potential. Posts may need to be purchased for areas where there are no trees or other features on which to mount cameras. Costs for camera batteries can be substantial and many camera models now require expensive lithium batteries. However, these lithium batteries will likely last an entire survey period or longer. Other equipment includes GPS units, tools to remove vegetation, and miscellaneous field gear including backpacks, clipboards, maps, compasses, etc. A large-scale study such as this will incur additional miscellaneous cost items that will need to be budgeted for.

Logistical Challenges

Implementing any ambitious camera-trapping effort overlapping private land requires contacting landowners, and possibly an arrangement for modest payment at the study's end if the units have received no vandalism or theft. This approach has been tried in Guatemala and Nicaragua with very good results. This kind of engagement is also helpful in developing an understanding of the area in general, and possibly identifying some interested local field assistants. Ideally, this kind of outreach to seek permissions to access land is done before camera installation such that cameras can be set up quickly and efficiently. Engagement while installing units may also be useful. The time required for this should be planned into the survey schedule (see [Occupancy Protocol](#) for more detail).

Capture-Recapture Modeling for Abundance and Density Estimation

Types of Abundance/Density Models

Camera trapping was first used in conjunction with capture-recapture models to estimate abundance and density for tigers (Karanth 1995, Karanth and Nichols 1998) and then modified later for jaguars (Kelly 2003, Wallace et al. 2003, Silver et al. 2004). These studies used the simplest type of abundance model, the closed-capture model, which is equivalent to the single-season occupancy model. Following similar analyses, genetic CR models for jaguars have only recently been used (Vynne et al. 2011, Wultsch 2013). Closed-capture models can be extended to multiple seasons in an open population framework following the “robust-design” capture-recapture approach (Pollock 1982). Additionally, Royle and Nichols (2003) linked heterogeneity in abundance to heterogeneity in detection to estimate local abundance of unmarked target species. Recently, Rich et al. (2014) used mark-resight models to estimate abundance of target species when only a portion of the population can be identified by natural marks. There are many more types of CR models with extensive available literature, but we deem the ones described and

discussed in more detail below the most useful for monitoring jaguars, sympatric predators, and prey for the NRU.

Closed-capture models—[Above](#) we describe the basic closed-capture model for abundance, which allows detection to vary by time, behavior, heterogeneity, or combinations of those factors (White et al. 1982). However, comparing abundances from one area or time period to another is not possible when sites have been surveyed with different numbers of camera traps using differently sized grids. In this case it is necessary to estimate density rather than abundance, usually described in numbers of jaguar per 100 km².

The “traditional approach” to density estimation entails using a closed-capture model implemented in either program CAPTURE or MARK and then dividing the resulting abundance estimate by an effective survey area. Program CAPTURE is not very flexible, but it does test for time, behavior, heterogeneity, combination effects, and closure violations, ultimately using a discriminant function analysis to rank models. Program MARK uses a maximum likelihood approach (i.e., to incorporate heterogeneity as a mixture model) and Akaike’s information criterion (AIC) model selection regime to rank the aforementioned models (Burnham and Anderson 2002). MARK is more flexible and allows use of covariates for individuals, such as sex or groupings by age or other factors.

Although CR models provide a statistically sound means of estimating abundance, estimating the effective survey area is problematic. Traditionally, researchers calculated half of the mean maximum distance moved ($\frac{1}{2}$ MMDM) between camera locations among all individuals recaptured at least once (Wilson and Anderson 1985, Karanth and Nichols 1998), as a proxy for home-range radius, and applied this buffer around the camera-trapping grid. Wulsch (2013) used this same technique but from scat sampling. Unfortunately, this buffer size is highly influenced by trap spacing and trapping grid size (Dillon and Kelly 2007, Maffei and Noss 2008). Additionally, for studies with both telemetry/GPS and camera-trap data, the $\frac{1}{2}$ MMDM has been shown to be a poor proxy for home-range radius (Soisalo and Cavalcanti 2006 - jaguars, Dillon and Kelly 2008 - ocelots, Sharma et al. 2010 - tigers). These traditional methods have been shown to produce biased density estimates that tend to overestimate jaguar density (Tobler and Powell 2013).

The SCR approach, on the other hand, makes use of the spatial information of individual captures to model individual movement and account for differential exposure of individuals to the trapping grid, thereby addressing a major source of individual heterogeneity in detection probability. The spatial location of captures is used to estimate activity centers (i.e., home-range centers) and the number of these centers is considered as the number of individuals in the study site. SCR models treat the trapping grid as embedded in a larger area, thus circumventing the problem of estimating an effective sampled area (Efford 2004, Royle and Young 2008). SCR models make some additional assumptions to the closed CR models, including that: 1) home ranges are stable during the survey, 2) activity centers are distributed randomly (Poisson

process), 3) home ranges are approximately circular, and 4) capture rate declines with distance away from the activity center following a predefined detection function, such as the half normal or hazard rate functions. SCR approaches provide a flexible framework where both trap-station-specific and individual covariates can be included in the models (Gardner et al. 2010b, Kéry et al. 2010). The SCR approach can be implemented using either maximum likelihood estimation techniques in Program DENSITY (Efford 2004) or the equivalent R package secr (Efford 2011), or in a Bayesian framework (Royle and Gardner 2011) in Program WinBUGS (Gilks et al. 1994) or JAGS (Plummer 2003), or the R package SPACECAP (Gopalaswamy et al. 2012c).

Because of these issues associated with using traditional density estimation techniques, we recommend using the SCR approach for jaguar density in this protocol. However, the data generated from this study can be analyzed by both traditional and SCR methods, allowing us to compare estimates to past studies that only used traditional methods. However, because we plan to cover large areas, the traditional and SCR methods may converge and our results may not be comparable to results from other studies using traditional methods if those studies used smaller survey areas. We expect our expanded number of camera stations and large spatial extent to result in accurate and unbiased jaguar density estimates.

Both traditional and SCR methods can be used on camera and genetic CR data. However, SCR methods were originally designed for surveys where detectors were stationary (e.g., camera traps), whereas for genetic data, there are no stationary detectors, as scat samples are collected anywhere they are found within the survey area. This issue can be resolved by placing a grid over the study area, such as a 2 km by 2 km grid, and assigning scat collected within that 2 km by 2 km area to the center of that grid – as if that was the stationary detector (Russell et al. 2012, Wultsch 2013). For animals such as jaguars, with large home ranges, this method is adequate for running SCR models on genetic data, as long as the size of the grid cells is smaller than individual movements. More recently, Royle et al. (2011) developed an SCR model for search-encounter data.

Robust-design, open population models—These models are an extension of the closed-capture models and are equivalent to multi-season models in the [Occupancy Protocol](#). They use capture history data on individual animals from surveys occurring over multiple years, following the “robust-design” CR approach (Pollock 1982, Pollock et al. 1990, Kendall and Nichols 1995, Kendall et al. 1997), which can be implemented in Program MARK. For the SCR framework, open models can readily be formulated in the WinBUGS language (e.g., Gardner et al. 2010a). We discuss these models more in the section on [Measuring Trends in Abundance/Density](#), below.

Mark-resight models—A limitation of photographic CR techniques above is that the species must be individually identifiable using natural markings, thus restricting sampling to species with unique coat patterns. Mark-resight models (Arnason et al. 1991, White and Shenk 2001, McClintock et al. 2009), on the other hand, provide a viable alternative to CR and SCR

techniques when only a portion of the photographed population is uniquely identifiable, usually by subtle, natural marks such as scars, ear nicks, tail kinks, and color patterns on legs (or botflies in Belize; Kelly et al. 2008). Photographic mark-resight techniques estimate abundance by incorporating photographs of marked (i.e., uniquely identifiable individuals), unmarked (i.e., individuals only identifiable to the species level), and marked but not identifiable individuals (McClintock et al. 2009, McClintock 2012 - <http://www.phidot.org/software/mark/docs/book>). The last classification occurs when an investigator determines that a photo is of a marked individual but cannot unambiguously identify the individual, usually due to a partial photo or blurry image. Mark-resight techniques assume the marked individuals are representative of the entire population in terms of detectability (McClintock et al. 2009, McClintock 2012). This is usually a reasonable assumption for naturally marked animals. Converting abundance estimates from mark-resight models into density follows the same ad hoc estimation (and suffers from the same disadvantages) of density using MMDM techniques in CR models. But recently, spatial mark-resight (SMR) models, similar to SECR models, were developed (Chandler and Royle 2013, Sollmann et al. 2013a, b) to address these limitations, and they have been successfully used for estimation of puma densities (Rich et al. 2014). We suggest using spatial mark-resight models on puma data that will be obtained from camera trapping to give us additional insight into how jaguars and pumas (competitors for similar food resources) co-vary across study sites.

Abundance-induced heterogeneity (Royle-Nichols) models—The Royle-Nichols model (Royle and Nichols 2003) makes use of the link between abundance and detection probability to estimate local abundance of target species. These models are based on the idea that heterogeneity in abundance generates heterogeneity in detection probability (i.e., the more locally abundant a species, the easier it is to detect at least 1 individual of that species during a survey). Based on this concept, this model uses the detection/non-detection data to estimate point abundance of the target species. This model is of particular interest to model prey abundance, because most prey species cannot be identified to the individual level. Jaguar prey is one of the most important limiting factors to jaguar presence and abundance, hence information on prey status is essential.

Pilot Data

Camera-trapping pilot-study data from parts of the NRU are currently available (see [Jaguar Status and Habitats in the Mexico Portion of the NRU](#)). However, it should be noted that our protocol calls for much larger trapping grids following recommendations of Tobler and Powell (2013) to obtain unbiased and precise estimates of jaguar density. The pilot study data that does exist should be used to guide the placement of additional camera traps in our proposed expanded abundance grids.

Measuring Trends in Abundance/Density

A major component in determining the status of a population is to determine trends in abundance or density over time. This gives us much more useful information than a single point estimate at

1 time period, and will enable us to determine if jaguar populations are increasing, decreasing, or remaining stable. We can also calculate population growth rates from multi-year abundance estimates, further enhancing our understanding of jaguar population dynamics. Robust-design, open population models (similar to multi-season occupancy models) provide the opportunity to model changes in abundance through time and determine population growth rates. They use capture history data on individual animals from surveys occurring over multiple years. With this approach, each year is considered a primary period with several secondary sampling periods (days or weeks) within each primary. Within each primary period, the population must be closed and hence follow CR assumptions. But from one primary period to another, the population is open such that individuals can enter or leave. This allows estimates of time-specific abundance, annual survival, and number of new recruits. Additionally, this approach explicitly models the effect of capture probability on capture history data and then can use reduced parameter models where certain parameters can be held constant over time (Lebreton et al. 1982), increasing the precision of survival estimates for any particular year (MacKenzie et al. 2005). This is important because some researchers have noted the relative imprecision of single-year abundance estimations from camera traps. For example, Karanth et al. (2006) were able to obtain more precise estimates and confirm that the tiger population in Nagarahole, India, was demographically viable with positive growth rate ($\lambda = 1.03$), high survival ($s = 0.77$), and high number of recruits.

We highly recommend using this multi-year camera trapping approach for jaguars in the NRU in order to obtain this demographic information. Surveys could be conducted annually for 3-month time periods as described above. Alternatively, we could also use multi-year scat surveys to do the same analyses if initial results reveal that scat collection obtains better information on jaguar abundance. However, because cameras will have already been purchased, it is likely that using camera trapping only may be more cost effective, especially if the 2 techniques give us similar results for closed-capture CR modeling.

Open population SCR models are not (yet) available in any of the user friendly software platforms (DENSITY, secr, SPACECAP), but can readily be formulated in WinBUGS (e.g., Gardner et al. 2010a). Robust-design kind of models, which estimate not only density in each primary period, but also survival and recruitment, are still in the process of being developed (Royle et al. 2014).

Conclusion

Surveying target areas via simultaneous large-scale camera trapping and scat-detection/molecular scatology surveys will give us a solid understand of baseline jaguar abundances and/or density across 4 distinctly different areas of the NRU. Extension of these capture-recapture surveys over multiple years also will enable determination of survival, recruitment, and population growth rates across the sites, information particularly useful for

assessing trends through time. The background information and techniques described in this abundance and density protocol can be used as a guide for planning such a project.

In addition to determining population abundance and density, jaguar status should also be assessed through population genetics. The scat samples collected through this protocol for genetic mark-recapture also can be used towards the goal of assessing genetic diversity, population structure, and genetic connectivity across the landscape (see [Population Genetics](#)). The in-depth, intensive surveys proposed here will give us some information on ranging behavior for individuals, but ranging information such as home-range size and habitat use patterns is best achieved through GPS collaring of individual jaguars (see [Demographic Parameters and Spatial Ecology](#)). The abundance surveys can aid in the process of GPS collaring by revealing where individuals repeatedly occur, and therefore the areas that can be targeted for trapping, thus increasing efficiency. The outlined abundance and density protocol is based on sound, up-to-date methods and analyses, will provide a substantial knowledge base on its own, and will feed into various other aspects of the overall monitoring plan, supplying needed information that will enhance jaguar conservation and management.

POPULATION GENETICS

Investigations into the genetic diversity, population structure, and demographic history of jaguars across most of their geographic range have revealed an absence of deep geographical subdivision and no evidence of bottlenecks, inferring historically high levels of gene flow (Eizirik et al. 2001, 2008, Ruiz-García et al. 2009, Culver and Hein 2013). In the context of gene flow into recent times and scant evidence for major historic-geographic differentiation, a range-wide connectivity analysis and interview-based occupancy modeling were used to identify and validate potential corridors connecting known populations and predicting travel routes between them (Rabinowitz and Zeller 2010, Zeller et al. 2011). Natural and anthropogenic boundaries (such as those encountered in the NRU) have been shown to affect population dynamics and structure for species with movements at the landscape level (e.g., Andreasen et al. 2012). Genetic population monitoring, including estimates of heterozygosity within and among populations, deviations from Hardy-Weinberg equilibrium, inbreeding within populations (F_{IS}), and subdivision among populations (F_{ST}), can contribute significantly to understanding population structure and movement of jaguars across large landscapes.

Noninvasive genetic methods provide researchers with new approaches to use landscape genetics to elucidate conservation challenges. These methods are used to document the presence, distribution, and abundance of rare, cryptic, and difficult to observe or handle species, including jaguars (Piggott and Taylor 2003). The most common sources of noninvasively-collected genetic material for studies of carnivores include museum samples (Johnson et al. 1998), hair (Kendall et al. 2009, Gardner et al. 2010*b*), scat (Kohn et al. 1995, Ernest et al. 2000, Farrell et al. 2001), and occasionally bone and connective tissue (King et al. 2008). The choice of which source is preferable depends on the question being asked and the species and population being studied.

Questions of an evolutionary nature can often be answered using museum samples if samples are available and if DNA is obtainable from the samples. Questions regarding current population structure, connectivity, gene flow, levels of inbreeding, or other population genetic parameters usually require contemporary samples such as hair or scat. Hair samples have been widely used for noninvasive research on 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, Kendall et al. 2009, Gardner et al. 2010*b*). In felids, scat is preferable to hair as studies have yielded a higher success rate with scat. This could be due to the lower amount of DNA in felid hairs as quantified by the Federal Bureau of Investigation, who determined a ten-fold lower yield of DNA from felid hairs compared to primate hairs (Bruce Budowle, University of North Texas Health Science Center, personal communication). The collection of jaguar hair using hair-snare sampling techniques in the wild has not been successful, attributed to the nature of felid hair, which are very short and fine compared to the coarser hair found in many canids, ursids, and mustelids (García-Alaníz et al. 2010, Portella et al. 2013). Additionally, compared to primate hair, felid hairs contain ten-fold less DNA per hair root (Victor David, National Cancer Institute, personal communication). Other sources of noninvasive samples include bone and

connective tissues. These samples can be obtained opportunistically from carcasses found in the environment, but also from predator scat as sample source for obtaining diet information (King et al. 2008).

Measuring jaguar occupancy and abundance provides a foundation for more intensive, noninvasive survey efforts to monitor jaguar population genetics. Recent advances in molecular genetics and the use of detection dogs to locate the scat of target species make fecal DNA analysis a promising and viable option for genetic monitoring. Population genetic monitoring has several objectives, including: 1) adding new detection locations for individuals detected on camera traps – this is important because camera traps are stationary, whereas surveys for scat samples cover a large area more completely, therefore the additional detections will give a better insight into jaguar distribution across the landscape; 2) detecting additional individuals to those known from cameras – this could be from detecting more individuals from scat than from photos or detecting different genders from scat than from photos; 3) investigating the basic genetic character of populations monitored (e.g., heterozygosity within and among populations, overall genetic diversity within and among populations, level of inbreeding within populations, comparing genetic diversity and inbreeding from populations monitored here with other published studies, differentiation of populations relative to other nearby populations); and 4) determining jaguar diet items found in scat using genetics, providing insight into preferred prey and/or livestock depredation – an important component in human-jaguar conflict.

Jaguar Scat Collection

Jaguar scat collection should be conducted: 1) opportunistically during setting and checking of remotely-triggered cameras as part of an occupancy or abundance survey; and 2) with the use of scat-detection dogs following a block design centered on locations of camera stations detecting jaguars.

Opportunistic Searches

Scats should be searched for opportunistically during the process of setting up and checking remotely-triggered camera stations, as cameras are set in locations that scat and other sign are usually found (e.g., canyon bottoms, natural funnel zones, along ridge lines, water holes, lesser used dirt roads). When time and logistics permit, opportunistic searches can be expanded to a wider area around the camera station (e.g., walking out a different travel route than the one used on the way in).

Scat Collection

All scats with large felid characteristics should be collected for genetic analysis because of the difficulty in visually differentiating jaguar and puma scat based on morphology (Foster et al. 2010). Specific data for each scat sample should be carefully documented and each sample should be labeled with a unique and obvious identifier (e.g., MacKay et al. 2008:221). As in the

[Occupancy Protocol](#) and the [Setting Cameras](#) section, a standardized protocol should be developed beforehand by people familiar with the study area, including clear descriptions of the data to be recorded. This will ensure that data are collected systematically and avoid confusion between field and laboratory personnel. Data for each scat should include, but are not limited to, date of collection, GPS coordinates, elevation, description of the substrate and habitat, scat length and diameter, a measure of vegetation density (e.g., can animals move around freely or are they likely to stay to defined paths), canopy cover, presence of a road or trail, presence of another kind of habitat edge (e.g., grassland/scrubland), presence of a stream/river, mountain ridge, gully, etc. The surrounding area should be photographed to document the scat morphology and vegetative community.

Each scat should be handled with unused latex gloves for surveyor safety and to prevent contamination of the sample. A variety of methods exist for preserving samples until genetic analyses are conducted. These include air drying at room temperature, freezing at -20°C , saturating and storing in a buffer solution, drying in a lyophilizer (i.e., a freeze dryer), storing in 70-100% ethanol or DETs buffer, drying and storing in silica or Drierite-based desiccant, or drying with an oven or ethanol then storing with silica desiccant. Each preservation method has its own advantages. The laboratory conducting the genetic analyses should be consulted to discuss options prior to sampling.

Portions of each scat should be collected in the field for preservation and transport for DNA isolation following Wultsch et al. (In review) or recommendations of the collaborating laboratory. The remaining scat material should be collected and dried or frozen for diet analyses (Scognamillo et al. 2003). Wultsch et al. (In review) evaluated the performance of 2 DNA storage techniques (DET's buffer [20% DMSO, 0.25M EDTA, 100mM Tris, pH 7.5, and NaCl to saturation (Seutin et al. 1991)] and 95% ethanol) for fecal DNA samples of jaguars and co-occurring Neotropical felids collected in Belize. For each fecal sample, approximately 0.5 mL fecal material was collected and stored at ambient temperature in 2 sterile 2-mL screw-top tubes filled with either DET's buffer or 95% ethanol at 1:≥4 volume scat-to-solution ratio. For each intact scat located, approximately 0.5 mL of fecal material was collected from 4 different locations (top, side, bottom, and inside) of the scat. Scat vials were stored for up to 8 months at room temperature until extraction. The authors reported DET's buffer was the superior fecal DNA preservation method with 44% higher (PCR) amplification success and 17% higher genotyping accuracy compared to 95% ethanol-stored samples.

Alternatively, the University of Arizona Jaguar Survey and Monitoring Project is drying and storing collected scat samples in Ziploc® bags with a 4:1 silica to scat weight ratio or freezing scat samples within 24-48 hours (Melanie Culver, University of Arizona, personal communication). In the laboratory, epithelial cells are obtained from the surface of the scat using a swabbing technique (see Rutledge et al. 2009, Wasser et al. 2011). Cotton applicators are saturated with PBS buffer and used to swab the surface of the individual scat sample. The swab

stick is then cut and placed in a labeled 2 ml tube containing 300 microliters (μ l) of ATL buffer (QIAGEN, Inc.).

Sampling Using Scat-Detection Dogs

We can increase scat collection rates over large, remote areas by using scent-detecting or scat-detection dogs (Smith et al. 2003, 2005, Wasser et al. 2004, Long et al. 2007, MacKay et al. 2008). Detection dogs commonly are trained and handled following protocols applied for scent-detecting and search-and-rescue dogs (MacKay et al. 2008). 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) and MacKay et al. (2008). Briefly, a scat-detection dog is trained to find scats from target species and to alert the dog handler to the specific location of each scat. Scat-detection dogs are trained to detect scats only from target species and to ignore scats from non-target species. A detection dog team typically consists of the dog, the handler, and an orienteer, all of whom require extensive training to function successfully as a team. Some researchers choose to train their own scat-detection teams while others choose to partner with one of several research laboratories or conservation organizations with experienced scat dog detection teams to conduct scat surveys.

Detections of jaguars by remotely triggered cameras can aid in focusing on target areas for scat surveys in order to increase the probability of locating jaguar scats. Scat-detection dogs, trained to locate jaguar and puma scat, can be deployed to find scat within those hexagons with jaguar detections. We recommend the use of scat dog(s) trained on jaguar and puma scats to avoid potential scat dog performance problems and additional opportunities afforded from collecting sympatric puma scats. Given the morphological similarities of jaguar and puma scats, a handler can erroneously reinforce, effectively training, a scat dog on scats from a non-target species (particularly puma). To avoid this potential challenge, we recommend training the scat dog(s) on both species. Additionally, diet information collected from both jaguar and puma scats would provide further insights into human-felid conflict involving livestock predation. An alternative method to avoid reinforcing non-target detections is to reward the scat dog on only known jaguar scats planted in the field by the handler. This approach would avoid the additional costs of genetically analyzing a large sample of puma scats, and precludes addressing questions related to sympatric jaguars and pumas, but may be advantageous if pumas greatly outnumber jaguars. Generally, the researcher will select and train dogs for the detection of scats. Training should consist of sufficient repetitions and complexity such that canines will be field ready, as determined by the researcher, prior to beginning field work.

For scat collection via scat-detection dog(s), we recommend targeting hexagons that have had detections of jaguars on remotely operated cameras and opportunistic encounters. Because this protocol does not attempt to estimate abundance in each hexagon, it is not constrained by obtaining enough captures and recaptures of individuals to conduct capture-recapture modeling.

Rather, this protocol attempts to obtain as many genetic samples as possible (preferably from different individuals) to better estimate genetic diversity and population genetic structure. Therefore, we suggest a flexible survey design where effort is standardized, but hexagons are searched opportunistically. We suggest conducting scat dog surveys using the established roads and trails, including the ones where cameras are placed, and other areas that jaguars are likely to use such as waterholes, rivers sides, canyons, and ridgelines. We suggest large spatial coverage, such as traversing the hexagon 5 to 6 times roughly from north to south or east to west, and ensuring that no 25-km² area that is accessible is totally missed, as this size is the smallest home range recorded for a female. If the hexagon is roughly 22 km across, this equates to 110-132 km of opportunistic searching per hexagon. Conservatively, scat dogs can cover 10 km per day, so this would equate to 10-13 days per hexagon. This protocol can be modified by lengthening or shortening surveys based on initial scat collection results. As a guide, at 2 relatively low density sites in Belize (i.e., 1-2 jaguars per 100 km²), Wultsch (2013) used a similar opportunistic searching regime and found a scat sample on average every 1.3-3.0 km of searching, but this did include both puma and jaguar samples. We suggest using GPS units to mark tracks searched and track distances traveled for ease in modifying search design following preliminary results.

Equipment and Costs

Refer to the [Equipment and Costs](#) section of the Abundance and Density section.

Laboratory Genetic Methods

Analyses of genetic samples are conducted by a DNA or conservation genetics laboratory selected at the beginning of the survey. Several factors should be considered in selecting a laboratory, including the lab's: 1) experience with jaguar or other felid scat samples collected in areas with similar conditions; 2) availability and ability to conduct or assist with post-genotyping statistical analyses (e.g., tests for genetic structuring); 3) ability to store samples over time; 4) protocols for evaluating contamination and errors; and 5) policies on data ownership and dissemination (Schwartz and Monfort 2008:251). The laboratory should be consulted on sample storage methods, labeling, tracking, and shipping genetic samples throughout the study design, sample collection, and genetic and data analyses phases of the research.

The DNA or conservation genetics laboratory selected will apply particular molecular genetic techniques depending on the expertise of laboratory to isolate DNA from scat samples; identify species, individuals, and gender; and conduct post-genotyping statistical analyses. The following are the suite of molecular genetic techniques used by the University of Arizona Jaguar Survey and Monitoring Project (Melanie Culver, University of Arizona, personal communication).

DNA Isolation From Scat

DNA is extracted using a QIAGEN stool kit following manufacturer's protocol (Qiagen, Valencia, CA). Extractions are (and should be) carried out in a room dedicated to low quantity

DNA sources to minimize contamination risk. Negative controls (no scat added) are (and should be) included in all DNA extractions and PCRs to test for contamination. The DNA extraction procedure is as follows: 33 µl of proteinase K (QIAGEN, Inc.) is added to the 2 ml tube and incubated at 70°C overnight. The swab is removed and 366 µl of AL buffer (QIAGEN, Inc.) is added, vortexed, and incubated at 70°C for 1 hour. Then 266 µl of ethanol is added and mixed by inverting. The DNeasy tissue kit (QIAGEN, Inc.) is used, following manufacturer's protocol for the remainder of the DNA purification.

Species Identification

The molecular genetic markers available for species identification in mammals almost exclusively include utilization of genes of the mitochondrial DNA. These are amplified using PCR and a DNA sequence is obtained and compared to known sequences to find a match to the species of origin. The ATP-6 region has been used to distinguish between jaguar and puma (Haag et al. 2009) and the mtDNA cytochrome b gene has been widely used to distinguish among all carnivores and mammals (Naidu et al. 2011). Pumas are the most widely distributed mammal in the western hemisphere and are abundant throughout the range of the NRU, and will be a common non-target species for scat collected, so either molecular marker strategy is appropriate for the purposes of species identification. However, the mtDNA cytochrome b strategy provides complete information on all samples, for example samples that are ocelot or canid, which also might be of interest. Also, because mtDNA cytochrome b amplifies all mammals, it can distinguish samples that contained some preserved DNA, even if it happens to be DNA of the prey species rather than the predator, which occasionally occurs.

Sequencing should be attempted with mtDNA cytochrome B primers (Farrell et al. 2000 or Verma and Singh 2003) using protocols described in Onorato et al. (2006) for the Farrell primers, or Naidu et al. (2011) for the Verma and Singh primers. Species identification of sequenced scats should be conducted by comparing DNA sequences obtained with known sequences of target species and with entries in GenBank using the BLAST program (National Center for Biotechnology Information).

The PCRs should be performed in a 20 µl final volume with a final concentration of: 12.3 µl of H₂O; 2.0 µl of 10x PCR Buffer (QIAGEN, Inc.); 0.8 µl of MgCl₂ (QIAGEN, Inc.); 0.4 µl dNTPs (QIAGEN, Inc.); 1.0 µl 0.05 % BSA (Sigma-Aldrich, St. Louis, MO, USA); 0.1 µl of Taq DNA Polymerase (QIAGEN, Inc.); 0.5 µl each of forward and reverse primers; and 4 µl of template DNA. The PCR conditions should consist of initial denaturation at 95°C for 10 minutes, followed by 35 cycles of denaturation at 95°C for 45 seconds, annealing at 51°C for 1 minute, extension at 72°C for 2 minutes, and a final extension step at 72°C for 10 minutes. All resulting PCR products should be cleaned with ExoSAP-IT (USB Corporation, Cleveland, OH, USA) and sequenced on an Automated DNA Analyzer.

Individual Identification

Felid microsatellite loci shown to be polymorphic in jaguars using PCR should be amplified to positively identify jaguar samples. The ten loci selected are shown to perform well in scat samples (FCA026, FCA075, FCA077, FCA090, FCA126, FCA139, FCA193, FCA211, FCA224, and FCA310; Menotti-Raymond et al. 1999) using the same PCR conditions as in Eizirik et al. (2001).

Costs

Refer to [Genetic Costs](#) section.

Analysis of Jaguar Scat Genetic Data

Species Identification

Sequence data should be edited using the program SEQUENCHER (version 3.0, Gene Codes Corp, Ann Arbor, Michigan) and compared to an existing database of mammal sequences to determine the species of origin for each sample. This analysis is used to identify jaguar versus other carnivore scat.

Individual Identification and Population Genetics

Microsatellite data should be scored and analyzed using the program GENOTYPER (version 1.1) (Applied Biosystems Inc.) to precisely calculate the sizes of the fragments and discard ambiguous or low-quality amplified genotypes. Once a composite genotype across all loci is compiled for each sample, for up to ten felid microsatellite DNA loci, pairwise genetic distances should be calculated among scat samples using the program MICROSAT (Minch et al. 1995). All pairs of samples with a distance of zero (i.e., complete sharing of microsatellite allelic data) should be presumed to have originated from the same individual, allowing an estimate of the number of unique individuals, which serves as a minimum number of jaguars for this study area. Estimates of heterozygosity within and among populations, deviations from Hardy-Weinberg equilibrium, inbreeding within populations (F_{IS}), and subdivision among populations (F_{ST}) should be made using the program ARLEQUIN (Excoffier and Lischer 2010).

DEMOGRAPHIC PARAMETERS AND SPATIAL ECOLOGY

While the broad brush of occupancy can provide a high quality sketch of where jaguars are and their relationship to resources, other questions relevant to jaguar recovery across the NRU can only be addressed through more intensive methods. A sound understanding of jaguar demographic characteristics and dispersal patterns will support landscape planning and management. Knowledge of how jaguars are organized in time and space, interact with each other and sympatric species, and obtain the resources on which they depend are all useful for developing finely-tuned conservation measures (Ceballos et al. 2005, Azevedo and Murray 2007a, Ripple et al. 2014), including the design of conservation practices that reduce the frequency of negative impacts caused by human-carnivore interactions (Treves and Karanth 2003)

Dispersal and Long-Distance Movements

Dispersal is usually a one-time behavior, often during adolescence but sometimes during adulthood, when an individual leaves its natal home range or its established home range, to establish its own, new home range (Turchin 1998). For example, using telemetry, Ausband and Moehrensclager (2009) studied swift fox (*Vulpes velox*) dispersal on the Blackfoot Reservation of Montana and documented straight-line distances moved of 43.1 to 190.9 km. Beier (1995) tracked dispersing juvenile pumas in fragmented habitat in California, elucidating the details of their use of habitat corridors and peninsulas.

Elbroch et al. (2009) documented a straight-line dispersal of 167 km by a male puma along the Chile-Argentina border. Atheyra et al. (2014) tracked the movements of a tigress through a human dominated landscape in India, obtaining extremely detailed information and a straight-line movement distance of 40 km. Fattebert et al. (2013) documented a male leopard (*Panthera pardus*) traversing 3 countries in Africa covering a minimum distance of 352.8 km. In northern Europe, Kojola et al. (2009) fitted 82 wolves with radio-collars, of which 15 carried a transmitter with a GPS and a mobile phone component (GSM; Televilt, Sweden, and Vectronic Aerospace, Germany) which provided 6 radio-locations daily. Dispersal distances, calculated as the straight-line distance between the middle of the capture territory and the middle of the wolves' new territories, exceeded 800 km for half the wolves with GPS collars.

Genetic tools can reveal patterns of abundance and dispersal as well. Gour et al. (2013) used non-invasive genetic data (from fecal samples) to establish the presence of 28 tigers in total, composed of 22 females and 6 males within the core area of the Pench tiger reserve. Through genetics from the scats, the authors examined patterns of male-biased dispersal and female philopatry, documenting female dispersal up to 26 km. It should be noted that non-invasive genetic methods (from fecal samples) have been used to estimate tiger abundance in India (Mondol et al. 2009, Gopaldaswamy et al. 2012b) and clearly can be expanded for more detailed population ecology studies.

Using invasive methods, Forbes and Boyd (1996) unraveled the origins of naturally colonizing wolves (*Canis lupus*) along the edges of Glacier National Park in Montana. Using tissue samples and hair samples, Proctor et al. (2004) used invasive methods in a study of gender-specific dispersal of grizzly bears (*Ursus arctos*) over a range of 100,000 km² straddling the rocky mountains of British Columbia, Alberta, Montana, and Idaho. They found that, on average, females and males dispersed 14.3 and 41.9 km from the center of their natal home range, respectively.

Telemetry and genetic studies requiring the capture and handling of jaguars are not recommended for NRU areas where rare individual animals are precariously reestablishing territories in historical but recently unoccupied jaguar range, like in secondary areas or portions of them. However, in areas where jaguars are more abundant and secure, such as the Sonora and Jalisco Core Areas of the NRU, capture-handling-telemetry based studies, which also yield genetic samples, may generate extremely useful ecological information for large landscape-level conservation planning and management.

Demography

Obtaining demographic data for jaguars is far more challenging than, for example, for African lions (*Panthera leo*), which inhabit relatively open habitats with good visibility that facilitates observations and data-collection to estimate survivorship and recruitment (Funston 2011, Mogensen et al. 2011, Brink et al. 2012, Ferreira et al. 2012). Through decades of hard work, Ruth et al. (2011) established an unprecedented understanding of puma survival and source-sink structure in Yellowstone's Northern Range, but also benefitted from the relatively open habitats, occasional roads, seasonal snow cover for tracking, and, in general, developed infrastructure and utilities the United States provides. Even the rugged Northern Rockies might provide some easier logistics than some of the larger jaguar habitats in the wild American tropics. Nonetheless, the wealth of studies on pumas suggest useful methods for jaguars (e.g., Hornocker 1970, Seidensticker et al. 1973, Lindzey et al. 1992, Ross and Jalkotzy 1992, Logan and Sweanor 2001, Robinson et al. 2008).

Calvalcanti and Gese (2009) conducted one of the most intensive jaguar telemetry studies (ten jaguars, 3 years) in the Pantanal of Brazil. The authors reported that home ranges were very unstable for both sexes, varying among seasons as well as individuals. In addition, site fidelity was also reported to vary considerably. These results emphasize that jaguars, once in a productive landscape, may be more social than previously thought for this species. Moreover, in such productive landscapes, spatial patterns of jaguars may be determined through territoriality rather than food limitation (Azevedo and Murray 2007a). These studies in the Pantanal region of Brazil may be relevant for understanding the spatial organization of jaguars and how spacing patterns may be affected by the availability of food resources in NRU recovery areas.

The vegetative density and extremely undeveloped areas without basic services that cover much of jaguar conservation range may find their logistical equivalent in the rugged mountain refuges that snow leopards (*Uncia uncia*) occupy, and are a partial reason for the lack of in-depth studies. However, the most relevant parallels for study design in much of the jaguar's range are likely found in tiger studies in tropical Asia (Karanth and Nichols 2002) and the furtive habits of jaguars may approximate those of leopards (Balme et al. 2009, Du Preez et al. 2014).

Logistical challenges notwithstanding, the methods for assessing demographic parameters, population ecology, spatial ecology, and dispersal are similar across all the above-mentioned species. Only long-term intensive research can reveal recruitment, mortality, emigration and immigration, and dispersal patterns. This requires correspondingly long funding commitments, and studies of this kind are recommended for the core areas of the NRU and for other significant core sites across the jaguar range.

In the context of jaguars returning to and residing in the southwestern United States, adaptive management and monitoring in the Sonora Core Area is particularly important. The configuration of the NRU, however, with Core Areas separated by Secondary Areas where jaguar status is less certain and secure, is a management and monitoring scenario echoed throughout jaguar range.

The collection of remotely triggered camera data to estimate occupancy or abundance can, in many cases, be extended to estimate key demographic parameters. In areas of high jaguar densities, biotelemetry (including very-high frequency [VHF] and GPS) provides opportunities to examine detailed demographic, spatial, and population ecology-related questions by enabling the estimation of survival, reproduction, dispersal, home range, and habitat selection (White and Garrott 1990, Millspaugh and Marzluff 2001, Miller et al. 2010). Methods used to capture and handle jaguars to deploy telemetry devices are presented in Polisar et al. (2014) and additional guidance on handling captured animals is provided in Proulx et al. (2012) and Foresman et al. (2012). Telemetry provides the ability to remotely monitor elusive, wide-ranging carnivores while they conduct their normal movements and activities, and, through active, near-continuous tracking, can reveal details that spatially stationary camera-trap stations will not. Genetic methods can be a powerful tool, too, to understand population characteristics, such as parent-offspring and dispersal movements, and, thus far, may have undeveloped potentials for even in-depth population data, such as survival and recruitment, logistics depending.

Survival and Recruitment

Camera-trap data in conjunction with open population capture-recapture models are used to estimate key demographic parameters in cases where camera-trap surveys can be repeated and individuals are identifiable over extended time periods, such as multiple seasons or years (Pollock 1982, Karanth et al. 2006, 2011b, Pollock et al. 2012). Open population models are used in long-term studies where, in addition to population sizes, the goal is to estimate

population losses (mortality and emigration) and gains (recruitment and immigration). The robust-design framework (Pollock 1982) combines sampling at 2 time scales where several short-term pulses of sampling (“secondary periods” that usually assume closure) are nested within long periods (“primary periods” during which the population is open). Analysis of capture-recapture data can be done using program MARK (White and Burnham 1999) and employing the “Recaptures Only” model to estimate apparent survival. Additionally, Gardner et al. (2010a) 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.

Karanth et al. (2011b) used the Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965) and Pollock’s (1982) robust-design model to estimate apparent survival, the latter of which nests 2 sampling scales: the primary being open and long-term, the secondary being the separate discrete closed sampling, which supports the primary. In this scenario, recruitment was estimated combining survival estimates and time-specific abundance. The details of distinguishing residents from transients, as well as distinguishing immigrants and emigrants, will not be handled here, but suffice to say the effort of Karanth et al. (2011b) covered ten consecutive years of sampling using a robust-design capture-recapture study to estimate time-specific abundance, survival, transience, recruitment, and trends. A long-term commitment in a core site is needed to estimate these parameters. Based on their experience, Karanth et al. (2011b) recommend increasing the number of camera traps, as well as the area sampled, to improve precision of the estimates. Quoting the authors “*in studies where a demographic monitoring program is really needed to address management or scientific questions, we believe that intermediate to long-term camera trap studies can be an effective approach.*” We recommend a combination of long-term capture-recapture studies in areas consistently occupied by jaguars throughout their range to assess population trends and basic vital rates, combined with an occupancy framework that examines jaguar distribution in the surrounding matrix.

Telemetry enables researchers to remotely locate and monitor marked individuals. These technologies provide opportunities to determine mortality rates, 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. Recent advances in tracking and telemetry technology have seen traditional VHF technologies eclipsed by the widespread use of GPS-enabled devices (Hebblewhite and Haydon 2010). GPS devices can collect fine-scale spatio-temporal location data systematically throughout the day and night. GPS telemetry can reduce the time investments needed to obtain animal locations and eliminate potential biases involved when collecting ground based telemetry locations. The technology has particular potential where road systems are absent, when animal movements are likely to surpass VHF tracking limitations, and where aerial and terrestrial access is limited due to security concerns.

Despite the advantages of GPS telemetry, Hebblewhite and Haydon (2010) issued several cautions. Because upfront costs, battery limitations, and failure rates are significantly higher for GPS devices, researchers may decide to deploy a smaller of GPS units to obtain more in-depth data sets on individuals at the risk of sacrificing the sample sizes needed to make population level inferences. These decisions may result in weaker study design, reduced sample sizes, and poorer statistical inference, relative to a study deploying VHF transmitters (Hebblewhite and Haydon 2010, Fieberg and Börger 2012).

As an example, studies of animal survival with known-fate collar data require more than 50-100 animals (Murray 2006, Hebblewhite and Haydon 2010). Schwartz et al. (2010) used data from 362 grizzly bears spanning 21 years to examine hazards affecting grizzly bear survival in the Greater Yellowstone Ecosystem. Smith et al. (2010) monitored survival of 711 radio-collared wolves between 1982 and 2004. Ruth et al. (2011) used data from 104 pumas to assess survival in Yellowstone's northern range before wolf reintroduction (1987-1994) and after wolf reintroductions (1998-2005). Goodrich et al. (2008) used data from 42 radio-collared Amur tigers between 1992-2005 to assess survival rates. Several of these data rich studies combine VHF and GPS technologies because they date back decades, but the cost of obtaining similar samples for equally meaningful survival estimates using GPS units is considerable.

Thus, estimates of population-level parameters may still be more precise when using VHF data, particularly if among-animal variability is substantial. Most top-end collars now provide both capabilities, allowing vast data collection via satellites while retaining the option for researchers to get close to the location and confirm habitat selection, kill characteristics, and mortality and its sources.

The 2 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 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. 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.

The 18-year-long study on pumas in Northern Yellowstone, initiated by M. Hornocker and K. Murphy, and summarized by Ruth et al. (2011), is instructive of the dedication and detail needed

to determine vital rates. Using a combination of track surveys in snow; captures of adults, subadults, and kittens; radio telemetry; ear tags; age estimates; VHF and GPS telemetry with mortality sensors; carcass inspections; necropsies; and on-ground close proximity locations complemented by GPS capabilities, adequate data were available to assess patterns of female and male survivorship and sources and sinks within a 3,779-km² mountain landscape, which, while focused largely in the intermediate elevations where prey was abundant, also contained some of the most rugged terrain in North America. This depth may not be possible in the Sonora and Jalisco Core Areas of the NRU, or in other areas across the jaguar's range, but the general recommendations derived for the survival parameters are as follows:

- Study areas can be defined by adult home ranges;
- Program MARK should be used to evaluate survivorship;
- Kitten, sub-adult, and male and female adult survivorship should be analyzed independently;
- Temporal covariates (e.g., drought months in semi-arid environments, flood months in others) should be examined;

Landscape/habitat characteristics should be examined, such as elevation, topographic roughness, predominant forest type, real or validated proxy measures of prey abundance, distance to communities and roads, and other relevant indices of wilderness, either aggregated or through specific parameters.

Hornocker (1970) and Seidensticker et al. (1973) pioneered puma studies in wild rugged terrain in Idaho, which likely matches the Sierra Madre in Mexico and therefore could be used as a model for collecting these data within some areas in the NRU. Data like these are obtained in increments, with a long-term commitment.

Home Range

The concept of a home range is one of the core concepts of modern spatial ecology. GPS telemetry technologies have allowed the collection of location data at an ever-increasing rate and accuracy, ushering in the development of new methods of data analysis for portraying space use, home ranges, and utilization distributions. Vendors of telemetry equipment include Lotek (Knopff et al. 2009, Chadwick et al. 2010, Inman et al. 2012), Telonics (Schwartz et al. 2006, Kojola et al. 2009, McCarthy et al. 2010, Ruth et al. 2010, Smith et al. 2010, Hojnowski et al. 2012, Inman et al. 2012, Coleman et al. 2013), Televilt, acquired by Followit (Kojola et al. 2009, Smith et al. 2010, Elbroch and Wittmer 2012, Inman et al. 2012), and African Wildlife Tracking (Tambling et al. 2010), but also see Advanced Telemetry Systems, Vectronics-Aerospace and NorthStar. Fuller and Fuller (2012) present the fundamentals of satellite telemetry. Selecting appropriate units involves tradeoffs between weight, data storage download characteristics, unit lifespan, cost, and research objectives.

With an ever-increasing number of techniques available, research questions must be designed to test theoretical predictions and avoid *post hoc* analyses with little power (Kie et al. 2010). Although intensive, large-scale camera-trap studies can and will obtain information which can be interpreted as home ranges and spatially explicit capture-recapture models may generate home-range estimates and related parameters as output, these studies are confined both by the stationary camera traps, and also the boundaries of the sampled area. The unbounded continuous space and series of points obtained through telemetry are far more appropriate for home-range estimates and understanding how individuals overlap, avoid each other, and spend time together. Camera-trap studies will provide similar data, but are confined to each and all the sampling stations, while telemetry tracking is continuous across space, providing more detail.

Minimum convex polygons (MCP), although widely used, provide little more than crude outlines of where an animal has been located (Hayne 1949, Powell 2000, 2012). Although conceptually simple and allowing for comparisons to earlier studies using MCPs, problems with the method are many, including discarding 90% of location data collected within the outer boundaries, thus emphasizing the often unstable outer boundary of a home range, and ignoring the internal structure of a home range.

Most modern home-range estimators produce a “utilization distribution” from location data describing the intensity of use of different areas by an animal. A utilization distribution is calculated as a probability density function, which describes the probability that an animal has been in any part of its home range (Hayne 1949, White and Garrott 1990). Kernel density estimators are now widely used to estimate home ranges (Laver and Kelly 2005). Band width selection is a critical, yet a difficult, aspect of developing a kernel estimator for animal home ranges (Silverman 1986). Band width can be chosen using location error, the radius of an animal’s perception, and other pertinent information, but must be chosen to fit the hypothesis being tested, the datasets, and other research goals (Powell 2012).

Alternatively, local convex-hull estimators are an important alternative to the widely used kernel estimators, especially when use of space has sharp boundaries (Getz and Wilmers 2004, Getz et al. 2007). Brownian bridges can be used to estimate the probability of an animal being at a specific location in between fixes by incorporating time-sequence information that is available with most data on animal locations (Horne et al. 2007, Kie et al. 2010, Powell 2012). Additionally, biased random bridges offer another approach to movement modeling that is not based on the assumption of constant, diffusive movements, and creates movement based kernel density estimates rather than locational-based kernel estimates (Benhamou 2011). Finally, model-supervised kernel smoothing (Matthiopoulos 2003) and mechanistic (Moorcroft and Lewis 2006) approaches to home ranges evaluate the underlying importance of habitats or landscape characteristics when the amount of time an animal spends in a location may not coincide with the importance of that location.

As with the selection of band width, selection of a home-range estimator must be chosen to fit the hypothesis being tested, the datasets, and other research goals. Traditional kernel home-range estimators can still be used to advance our knowledge of why animals have evolved the behaviors and use of space documented (Kie et al. 2010). The `adehabitatHR` package (Calenge 2011) for the R statistical environment (R Core Team 2014) is one of many software packages used to estimate MCPs, kernels, local-convex hulls, and Brownian bridges.

GPS telemetry yields large data sets with less sampling limitations and bias than ground-tracking. In many cases, the understanding of time-specific resource availability has not kept pace with this enhanced resolution. This is particularly an issue if remotely accessible data means research biologists have no field sense of their study area, or if the resources important to study animals remain understood only at far coarser level than the telemetry data. Hebblewhite and Haydon (2010) advocate using the time saved on radio-tracking triangulations and flights for a better resolution picture of the habitat and resources important to the study animals, stating that “ecologists should become better in matching temporally varying estimates of resource availability at the same time scale as animal movements.”

Habitat Selection

The concept of “habitat” is based on the classic notion of the ecological niche, whereby animals select the resources and conditions that increase fitness (Hall et al. 1997, Morrison 2001, Sinclair et al. 2005, Mitchell and Hebblewhite 2012). The niche is a property of a species, includes abiotic and biotic components, is related to fitness, and includes long temporal and large spatial scales. Several studies have examined habitat use of jaguars, including, but not limited to: Crawshaw and Quigley (1991), Núñez et al. (2002), Cavalcanti (2008), and Conde et al. (2010). These studies provide some insight into *where* jaguars live, but knowing *why* animals live where they do can lead to robust understanding, effective management, and long-term conservation (Gavin 1991). The best understanding of jaguar habitat will explicitly relate resources to the survival and reproduction of jaguars (Mitchell and Hebblewhite 2012).

Johnson (1980) proposed a hierarchy of selection processes in which first-order selection is the physical or geographical range of the species. Within that range, second-order selection is the home-range of an individual or social group (e.g. an individual jaguar or a wolf pack). Third order selection is the use of habitat components within a home range. Fourth order selection could be the specific procurement of food items within a habitat sub-component (e.g. capybara in a stream edge, or peccary in adjacent gallery forest). The boundaries of these orders are less important than recognizing that there is a hierarchical continuum of scales. Proctor et al. (2012) used genetic analyses from 3,134 bears and radio-telemetry data from 792 bears to examine grizzly bear population fragmentation across 1,000,000 km² of western Canada, the northern United States and southern Alaska. This approximates a first-order selection scale. Studies examining grizzly and black bear seasonal habitat preferences (Carter et al. 2010, Graham et al. 2010, Nielsen et al. 2010, Milakovic et al. 2012) or seasonal shifts in jaguar home ranges

(Cavalcanti and Gese 2009) could be viewed as third order selection on an annual or lifetime perspective and second order selection on a seasonal time frame. Zeller et al. (2014) proposed the use of continuum of scales when examining habitat selection, and used data from 8 collared pumas and gradients of criteria to differentiate habitats selected during movements versus during relatively stationary resource use.

Roads may be a component of jaguar habitat and can be characterized by year built, construction class (width of road surface and width of cleared land) and traffic volume data (Graham et al. 2010). Where anthropogenic factors are significant, human density, types of roads, and distance to roads and/or communities should be factored into habitat selection models.

Sampling Designs

Almost all habitat-selection studies follow one of two sampling protocols: 1) comparing used resources with unused resources, or 2) comparing used resources with available resources (Manley et al. 2002). Used-unused (presence-absence) designs are perhaps the most straight forward for habitat-selection studies. Logistic regression is a common statistical framework for comparison, whereby a binary response variable represents used and unused resources (Hosmer and Lemeshow 2000). Data relevant to investigating jaguar habitat selection using this design include remote-camera trapping (animals are either photographed or not-photographed) or mark-recapture trapping through photographing and DNA sampling. Using aerial track surveys in snow for large-scale (3,851 hexagonal 100 km² sampling units) occupancy sampling in northern Ontario, Bowman et al. (2010) found wolf occupancy higher in sample units with high caribou (*Rangifer tarandus*) and moose (*Alces americanus*) occupancy. In a similar fashion, prey occupancy may interact with other environmental characteristics to influence jaguar distribution. Sunarto et al. (2012, 2013) made recommendations on data to collect at camera trap stations to characterize those micro-sites. We make these available in [Appendix 6](#). Details on modeling environmental covariates are provided in the Covariates subsection in [Presence-Absence and Occupancy](#) and [Abundance and Density](#).

Use-available (presence-only) designs are among the most common method used for analysis of habitat selection (Mitchell and Hebblewhite 2012). The design only includes information about where animals used habitats (Pearce and Boyce 2006). Radio-telemetry data are perhaps the most common for the use-available design. DNA sampling has been used for use-availability resource selection (Vynne et al. 2011), but scat locations may have biases that constrain their utility as an indication of the continuum of microsites important for carnivore fitness. They may be best handled in a presence-absence framework. Abundant repeated locations of radio-marked animals identify areas used, and a random sample or census of resources within an animal's home range identify available resources (Manley et al. 2002).

Availability Data

Inferences from habitat-selection modeling with the use-availability design are contingent on how availability is defined (Beyer et al. 2010, Mitchell and Hebblewhite 2012). No completely objective means of calculating availability exist; however, recommendations exist in the habitat-selection literature.

The concept of availability depends on the spatial scale at which selection is investigated. Fundamental to an understanding of how and why jaguars use particular areas is mapping of availability at a scale relevant to jaguars. Many studies have sampled availability with a set of random locations within an animal's home range (i.e., 3rd order selection; Johnson 1980). The implicit assumption that animals can move anywhere within their home ranges at any time between successive locations may not hold in all circumstances. Thus, movements and habitat selection are intrinsically linked. Compton et al. (2002) defined availability as the area each individual could have reached from each location based on its history of movements. Used and available locations were compared using a conditional logistic model (Hosmer and Lemeshow 2000). Although Compton et al. (2002) studied wood turtles, the technique has applicability to jaguars.

Covariates

Many studies of the habitat ecology of carnivores describe habitat simply as the places or prevailing conditions where animals are found (Mitchell and Hebblewhite 2012). This descriptive approach relates occurrence, use, or selection by carnivores to vegetation communities, digital elevation models, remote sensing variables, and other types of spatial variables easily obtained in a GIS framework. These variables are used as surrogates for measures of resources, such as specific food types, which contribute directly to fitness. The use of surrogates relies on assumptions about their relationship to what they represent and, in many circumstances, could be violated. The assumption that variables reflecting vegetation communities are surrogates for availability of plant forage for omnivores or of prey for carnivores are often unwarranted and infrequently tested (Mitchell and Hebblewhite 2012). The inability of these habitat models to explain carnivore behavior argues strongly for considering prey resources explicitly.

Relating prey abundance and distribution to vegetation types and physical characteristics allows a better understanding of why felids use space the way that they do (Karanth and Sunquist 1992, Karanth 1993, Polis et al. 2003, Scognamillo et al. 2003, Karanth et al. 2004, Azevedo and Murray 2007a, Hojnowski et al. 2012). We suggest that habitat definitions for jaguars include abundance and distribution of prey. Because rigorous estimates of prey abundance and biomass are labor intensive, defining the scale of sampling is an important consideration in quantifying prey biomass and relating it to habitat characteristics and anthropogenic factors. Methods for occupancy-based estimations of prey density using field sign are provided in Gopalaswamy et al.

(2012a). Sampling and analysis considerations for distance sampling methods based on direct observations are provided in Buckland et al. (2001, 2008). Physical characteristics, such as proximity to publically-accessible roads or human settlements, still may be important predictors of jaguar survival, and therefore also should be included when defining jaguar habitat.

Data Analysis

Resource selection functions (RSFs) have gained prominence in habitat-selection studies (Boyce and McDonald 1999, Manley et al. 2002). Manley et al. (2002) defined RSFs as any function that is proportional to the probability of an animal's use. RSFs are commonly used to develop posteriori statistical models to describe habitat, but they also lend themselves to hypothesis testing. Hypotheses about the relative importance of specific habitat features and combinations of those features can be tested by evaluating competing multivariate RSF models using AIC (Burnham and Anderson 2002).

However, Mitchell and Hebblewhite (2012) offer:

...the uncritical use of surrogates, particularly given the rapid growth of remotely sensed land-cover data, computing power, and the use of sophisticated analytical techniques, has produced a large number of studies whose definition of habitat would seem to be “throw a bunch of conveniently available environmental variables into the statistical hopper and see what pops out.”

Alternatively, Mitchell and Hebblewhite (2012) recommend testing meaningful, *a priori* hypotheses linked to fitness parameters that provide stronger inferences on the cause-and-effect relationships that underlie habitat selection.

Cross-validation, both with internal and external data, is necessary to test the predictive accuracy and utility of a habitat model (Roloff et al. 2001, Boyce et al. 2002, Johnson and Gillingham 2005, Johnson et al. 2006). Cross-validation also provides insights into how robust a habitat model is to aspects of study design, such as autocorrelation, non-independence, multicollinearity, and sample size (Manley et al. 2002, Johnson and Gillingham 2005). Internal cross-validation uses data used to generate the model to test different “versions” of the model in a k-fold procedure. Briefly, a researcher divides data into k-partitions and cross-validates the predictive capacity between observed frequency of use and predictive frequency of use across the partitions of the data. A superior alternative to internal cross-validation is external validation, whereby a comparison of model predictions to independent data (collected in different years and study areas) are used to test model generality, accuracy, and precision.

Examples

In order to clarify second order habitat selection, in a 4,900 km² study area in North Carolina, Dellinger et al. (2013) used adaptive nearest neighbor convex hull methods to construct 95%

home ranges for 20 red wolves (*Canis rufus*) carrying Lotek GPS 4400S radio collars. Using rarefaction curves the authors determined that home range estimates had stabilized if size increased < 5% with each additional week for at least twelve weeks. The authors used RSFs that assumed habitat selection was indicated by comparing known points (GPS locations) to random available locations across the landscape. The number of randomly selected locations equaled the number of used locations. All used or available locations were combined across individuals (conceptually a pack of red wolves would approximate an individual jaguar). The authors categorized six types of land cover types, three natural, and three human-altered habitats, as well as biologically meaningful interactions (land-cover type by distance to roads, land-cover type by human density, and distance to roads by human density). One of the conclusions of this second order examination of habitat selection was that, in the absence of high human density (threats), red wolves selected for human-altered habitats, such as agricultural fields and regenerating logged forests that were potentially rich in prey such as white-tailed deer. Low volume dirt and gravel roads in the study area were not avoided. However, where human densities and hence potential threats increased, the use of natural habitats including old growth forest, also increased.

In an effort to understand the impacts of major road work on gray wolves (*Canis lupus*) in 12,907 km² area in Quebec, Canada, Lesmerises et al. (2013) tracked 22 wolves belonging to three packs along three major roads using GPS collars (Lotek 3300SW and Telonics GPS-4580), acquiring fixes every four hours year round. For habitat availability, maps at the 1:20,000 scale were classified into ten categories of forest type. Roads were described as before, during (active/inactive), and after. RSFs were used to estimate the relative probability of use of each habitat feature. Home ranges were calculated as 95% minimum convex polygons (MCPs) and for each wolf as many random points as GPS locations were distributed within the MCP to obtain an assessment of habitat suitability and determine the habitat category where the GPS location and the random point were found. The distance to nearest paved road was calculated for both points within a 5-km threshold. The RSF was developed to integrate the interaction between the shortest distances to paved road with the state of the road at that nearest point. “Before” was used as a reference. Mixed-effects models were used with crossing rate as the dependent variable and road state, annual period, daily period, and their interactions among the fixed effects. Wolf responses were primarily driven by the level of human activity, but crossing rate also decreased as road enlargement increased. Wolves still crossed enlarged highway, but at reduced rates, and were likely to use forested areas as hiding cover, crossing the road at night.

In a very remote, relatively natural 7,400 km² study area in Northern British Columbia, Milakovic et al. (2011) monitored 26 wolves from five packs using GPS collars (Simplex-Televilt). GPS locations were compared to randomly selected locations within the 95% MCP of each wolf pack (equivalent of an individual jaguar) across five seasons based on biological criteria for wolves. Habitat values were based on readily available biophysical characteristics (land cover, elevation, and aspect) that were reduced to 10 cover types and 4 aspect categories, as well as a categorical fragmentation index. Concurrently, GPS data were collected on moose,

elk (*Cervus elaphus*), Stone's sheep (*Ovis dalli stonei*), and caribou, and logistic regression models for these species incorporated locations, land cover class, elevation, aspect, fragmentation, vegetation biomass and quality and an index of predation risk. The prey selection surfaces were incorporated into wolf selection models, competing with those based solely on biophysical parameters, running the wolf selection models for each prey item separately and then all four pooled. On a global level, wolves selected for shrub-communities and high fragmentation across all the seasons, although each pack demonstrated individual habitat selection characteristics. Wolves did not select the same areas that the four prey species did (the latter also selecting areas to avoid predation risks), but may have selected opportunistic travel routes between land cover classes that maximized encounters with diverse prey.

In the same study area as above, Milakovic et al. (2012) used data from 27 grizzly bears fitted with GPS collars (Simplex, Televilt), using RSFs (Manley et al. 2002) to model habitat selection. The authors defined habitat availability within 95% MCP home ranges, and identified three seasons based on plant phenology, pooling seasonal data for each bear across years, using 50 points as a minimum to satisfy sample size and aid model differentiation. Land cover and topographical variables were 25 m resolution raster data, and included 10 land cover classes, three categories of fragmentation. Analyses included selection models developed for ungulate prey in global seasonal selection models across all bears and for each individual bear. Across seasons, grizzly bears as a group avoided conifer stands and low fragmentation areas and selected for burned vegetation classes and high fragmentation areas, with the interpretation being that these areas provided high quality forage and potential encounters with ungulate prey.

Jaguars differ from wolves in being solitary, stealth hunters rather than coursing hunters. Unlike grizzly bears, they are not linked to plant phenology due to an omnivorous diet. However, their mammalian prey may be linked with plant phenology patterns. The above studies demonstrate that selection may be positive for habitats where the risks of being killed by humans are lowest. Nielsen et al. (2010) recommended more attention be given to food resources affecting bottom-up regulation of populations, while top-down limitations be integrated into habitat models through mortality risk. Their recommendations were based on 42,853 GPS telemetry locations from 44 grizzly bears used to assess predictive habitat quality models that were developed from 642 land cover stratified random field plots for plant food quality, 51 field-visited ungulate kill locations, 1,032 field visits to GPS fix locations, and complemented by data from a hair-snag mark-recapture study.

Conde et al. (2010) reduced 5,246 GPS locations from three adult females and three adult males in the Selva Maya of Mexico just north of Guatemala by filtered points through 72 hour intervals to reduce autocorrelation, resulting in 218 independent female locations and 226 independent male locations. A random sample of 10,000 pseudo-absences were selected from each individual's home range. Habitat variables used in generalized linear models included those drawn from geo-spatial data (five general land cover types, density of paved and unpaved roads, distance to roads) and sex of study animals. Distance to population centers and human

population densities were not included due to strong correlations with road proximity. The model that included interactions between sex and road distance and between gender and land cover had lowest AIC values, runner up models included sex and landcover interactions, and the model that excluded gender performed poorly. Both male and female jaguars showed a preference for tall forest (which in the Selva Maya has a higher diversity of mast producing trees as well as less seasonal flooding than short forest). Females avoided two disturbed land cover types, cattle ranching and secondary vegetation. Males showed a tendency to use agricultural land and cattle ranching in proportion to availability. The probability of female occurrence increased away from roads, while roads had a negligible effect on male occurrence. To assess predictive capabilities of the model, the authors used 149 telemetry locations from five jaguars not included in model development. Cross validation showed reasonable discrimination by the selected model, with results indicating substantial agreement between observed and predicted values, and the percentage of points correctly placed ranging from 85.5 to 96.4, testimony to intra-specific differences in habitat selection.

Kertson et al. (2011) used data from GPS and VHF collars on 27 pumas in a 3,500 km² study area in western Washington in the United States to evaluate use of space and movements in the wildland-urban interface. In a RUF, use is a continuous variable represented by a utilization distribution, which is related to landscape features using a multivariate resource utilization function (RUF). This identifies the individual animal as the experimental unit, measures use continuously instead of discretely, and accounts for variable intensity of use. The landscape characteristics used in modeling were hypothesized as good predictors of presence of prey and cover, and measures of anthropogenic land change. However no direct measures of prey or stalking cover were part of the six variables used. The relative importance of landscape features differed between all pumas and years, with no two pumas using the landscape the same way. Despite significant variation in resource use at the individual level, when cross-validated, the population wide RUF accurately predicted puma and human interactions. The population level conclusions aligned with the author's local knowledge of puma natural history, but they speculated that the large variability among individual pumas may have been a result of some landscape features being poor surrogates, and suggested that an ideal model of puma space use would include direct measures of cover and prey availability.

In a 4,089 km² study area in the Santa Monica Mountains of California, Zeller et al. (2014) used data from eight pumas fitted with GPS collars (Lotek 4400) programmed to acquire locational fixes every five minutes. The authors used a range of threshold distances moved between these fixes to determine behavioral state and thus examine potential differences between resource use and movement locations and thus, differences in habitat selection in behavioral states.

Wells et al. (2014) used GPS collars (GPS plus collar v6 Vetric-Aerospace) on mountain goats (*Oreamnas americanus*) fitted with accelerometers that recorded count data at five-minute intervals based on movement of the GPS collar in X and Y axes to identify behaviors of interest. This impressive hardware was used in conjunction with Brownian Bridge Synoptic Models

(BBSM) to delineate and evaluate mountain conservation and management planning. The step-wise BBSM approach uses the serial nature of telemetry data to establish independence, rather than applying arbitrary thresholds. At each step along a movement path, the BBSM defines an underlying distribution of availability. The probabilities of availabilities are higher in the direction of persistent movement. This reduces the error of pairing random points with use points when in fact telemetry data may indicate a persistent movement in one direction. The BBSM is a fine-scaled approach that joins the analytical tools of RSFs that can help researchers and managers effectively use GPS collar location data to obtain maximize insights into the details of habitat selection at the individual and population levels.

Conclusion

Thoughtful, *a priori* questions are paramount in designing habitat selection studies and guiding the scale of the mapping and sampling needed to address questions. Jaguars use large areas, but may concentrate their activity in specific parts of enormous home ranges. What are the characteristics and significance of those areas? A jaguar's use of space relates to patterns of prey distribution and abundance. What environmental factors are driving the spatial patterns of secondary productivity? Risk and high mortality might also result in apparent habitat selection patterns. What physical characteristics are the most relevant for survival and recruitment? These questions will help define the biological and physical parameters to include when examining habitat selection in a meaningful way. Developing hypotheses *a priori* will clarify what supporting data are needed.

Well-chosen environmental covariates in occupancy modeling will provide insights on the parameters important to confront threats for existing jaguar populations and facilitate range expansion. Collecting environmental data at each station during camera-trapping CR studies can identify habitat characteristics associated with increased capture rates. However, camera trap studies of any type have the inherent limitation that they are sampling specific points that animals pass by, rather than along the continuum of their movements. Intensive telemetry studies provide the best movement data, and GPS collars provide abundant, unbiased location data for high-definition habitat selection studies.

Zeller et al. (2014) noted that animals usually select habitats and resources along a continuum of scales and that selection may change depending on behavioral states. The random selection of availability points employed in RSFs can satisfy questions about third order selection. RUFs and BBSM can track individual animal selection patterns, employing directional selection rather than a cloud of points in a home range that, in all likelihood have linear relationships along gradients of use intensity. Technological advances have increased our ability to examine jaguar habitat use at multiple higher-definition scales, yet, across vast stretches of jaguar habitat protected area enforcement and wildlife law enforcement remain weak. On the large scale of jaguar range and landscapes, effecting conservation may require that considerable conservation resources and efforts are directed at the multiple social and administrative levels needed to accomplish on-the-

ground advancements. The continuum of habitat selection information obtained through 1) environmental covariates in occupancy surveys, 2) covariates in CRC studies, and/or 3) high resolution telemetry based RSF, RUF, and BBSM habitat selection studies can inform these efforts.

DATA CAPTURE AND CURATION

Collection and export

Jaguars may be detected using a wide variety of techniques, such as those described in this document. Each technique generates particular types and formats of data, which can vary depending on the software used to capture and manage them. These data can then be used in particular types of analyses, such as:

- camera trap monitoring;
- radio/GPS collar or other telemetry techniques;
- scat dog detection;
- transect surveys;
- historical and museum specimen records;
- layperson or citizen-science reports.

As a general principle, it is both advisable and realistic to collect and maintain these raw data using the methods commonly associated with each technique, rather than shoehorn them early into one-size-fits-all schema inappropriate to the data or the intended analyses. For example, camera trap data are often produced with the help of software that ships with particular camera models (e.g., BuckView with Reconyx cameras:

<http://images.reconyx.com/file/BuckViewUserGuide.pdf>) or open-source applications such as OpenDeskTEAM (an offshoot of <http://www.teamnetwork.org/help-deskteam>) and CameraBase (<http://www.atrium-biodiversity.org/tools/camerabase/>). Other techniques commonly employ spreadsheets in formats comfortable to individual researchers for particular applications.

Each technique should use the most efficient and tested method and format, *as long as it is capable of being easily exported or converted*. The ideal is to collect and manage data for a particular study in the easiest and most cost-effective manner possible, and then with equal ease be able to export it to a format capable of being compared with or integrated into other datasets.

Important considerations are that raw data (photos) be backed up prior to being sorted and analyzed, and that the analyzed photos be subsequently backed up for long term/permanent storage.

Converting data to a common standard is important for any higher-level analysis that involves synthesizing and analyzing data collected using different techniques across large areas and swaths of time. Estimating jaguar populations in NRU Core and Secondary Areas based on habitat-correlated densities depends on being able to establish a common set of accepted point observations to correlate with various habitat variables.

Standardization and aggregation

The Wildlife Conservation Society, with funding and collaboration from USFWS, has created an online jaguar observation database, available at <http://jaguardata.info/>, as a repository for all jaguar observation data, collected using any technique (Figure 10). The database:

- maintains a central authoritative version of standardized data, with integrated geographic information, providing anybody with web access maps and downloadable data they can be sure are the latest comprehensive versions and cite in publications;
- provides quick and easy access to customized sets of observations that match whatever criteria are important to particular users;
- allows multiple editors access to add, edit, or delete data and track change history, using a robust account and security system;
- uses an event-record structure (Sanderson and Fisher, 2011) that preserves *all* records of a given jaguar detection, not just the records considered authoritative;
- is capable of incorporating detections with all levels of geographic specificity: specific lat/long coordinates, polygons for detections attributable to an area but not a specific point, and even no geographic data.

Ingestion and Editing

Manual Editing

For accessibility by citizen scientists and/or laypersons, a web-accessible platform for sorting and analyzing data collected has great advantages. The online database provides a system of user accounts that allows an administrator to create, edit access rights for, and delete accounts to be used by designated editors. Editors can then add, edit, and delete events (i.e., observations or detections), the records that provide the evidence for the events, bibliographic information for those records (using the Zotero online bibliographic software:

https://www.zotero.org/groups/jaguars_in_the_southwest/items), and geographic and attribute information about the records. See Figure 11-15 for screenshots of how the application functions.

Automated Ingestion

For relatively small amounts of data, such as those from historical records, individual layperson reports, and studies involving small numbers of events, the existing observation editing interface performs well. For ingesting larger datasets, tools will be added (contingent upon funding) to the database administrative interface that will allow an editor to:

1. *Upload and process simple tabular data.* A standard template for the table in either csv or xls format is in the process of being specified, provisionally with the columns outlined in [Figure 9](#).

In order to ingest data, data will need to be converted from the system used to collect it into the standard, either via simple spreadsheet manipulation or via an export operation from collection software (e.g., CameraBase, OpenDeskTEAM). Values for *identity_type*, *lifestage_type*, and *sex_type* will be drawn from authoritative tables reflecting the latest types in the central database.

2. *Specify spatial and temporal distinction.* Larger datasets collected via modern scientific techniques such as camera trap and telemetry surveys often include multiple raw data points representing a single observation. Several images might be fired by a single camera trap trigger, for example, that a researcher wants to consider a single observation; similarly, many GPS-collar records of a jaguar might be collected from the same geographic point. The interface will provide a way to aggregate records into observation events according to a temporal threshold (e.g., camera trap records with timestamps \leq 60 minutes apart) and/or a spatial threshold (e.g., radio-collar records with locations \geq 3 km apart).
3. *Attach raw data attachments.* The interface will allow an editor to upload or link to the raw data that served as the basis for a set of observations, to preserve in a central location a copy of the original data that was converted or exported for inclusion in the standardized database structure. For example, an editor might attach a MySQL dump exported from OpenDeskTEAM for a season's camera trap survey.

RECOMMENDATIONS AND GUIDELINES FOR NORTHWESTERN RECOVERY UNIT AND BEYOND

Because jaguars occur across approximately 50% of their historical range, they may appear secure. The species' adaptability to semi-arid scrub, humid forests, and flooded swamps with forest islands imparts some insurance. Some jaguar conservation units are vast and contain hundreds of jaguars. Some contain thousands of jaguars. However, the fragility of jaguar status becomes clear every time the passive protection provided by poor access and low human population density rapidly melts as pastures and towns replace wild areas and jaguars. On the edge of human and jaguar contact, mortality rates can be stunning. In the matrix of effective conservation areas and areas experiencing rapid decreases, common measures are needed. How are jaguars doing range wide? Are they decreasing, increasing, or remaining stable?

Assessing the status of jaguars that occupy huge 10,000-100,000 km² source areas requires cost-effective designs and metrics. As a result, the monitoring protocol that we present for the extreme northern edge of jaguar range is designed to address a range of situations. Although designed for the Mexico-USA NRU, the protocol combines the experience of researchers who have worked on jaguars in Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Venezuela, Ecuador, Bolivia, Paraguay, Argentina, and Brazil. The intent is versatile guidance to assess jaguars in the NRU and beyond.

At the core of recommendations for extremely large areas like the NRU is monitoring occupancy. Occupancy surveys can be used to evaluate the spatial distribution or estimate the proportion of a given area occupied by jaguars and jaguar prey. This tool can provide a low-cost, effective evaluation of where jaguars are across large landscapes and trends across time and space. It provides indirect measures of jaguar abundance and opportunities to test, on a grand scale, the influence of covariates of biological and management importance (such as vegetation types, altitudes, topographical relief, prey abundance, livestock frequency, and human influences (proximity to open-access roads and towns)). Through occupancy sampling, we will begin to understand exactly where jaguars are, and why they are there, while establishing a baseline for long-term monitoring.

Guidance for occupancy field sampling and analyses, including how to measure trends, is outlined in the section titled [Presence-Absence and Occupancy](#). We recommend sample units of 500km², based on estimated male home ranges in the NRU to reduce auto-correlation and assess occupancy in a biologically meaningful way. We recommend assessing 50% of an area of interest to ensure adequate data are collected for reliable occupancy modeling. However, this could be reduced to 30% in subsequent surveys based on experience and objectives. Doing this right will require pilot studies to evaluate and refine methods. Evaluating occupancy can be done with either camera traps or using sign. Based on our knowledge of the NRU we have recommended camera traps. Elsewhere in jaguar range, sign-based surveys might provide quicker, more efficient results. We provide guidance for both.

Constraining surveys to the dry season potentially reduces variation due to jaguars making seasonal movements. It also reduces camera trap malfunctions due to moisture. Sign surveys may benefit from moist substrates, and thus, best be done in a wet season. Either way, constraining surveys to a single climatic season will help approximate constant occupancy states. Repeated single-season occupancy surveys can be assessed using a multi-season model for trends, and/or multiple surveys can be combined and a time effect included in the predictor for occupancy. We provide guidance on study duration, camera placement, data to collect at each station, data processing and storage, analysis, costs, and how to conduct power analyses on the suggested pilot studies. Large scale occupancy surveys are recommended to assess the status of jaguars range wide.

While occupancy provides a broad brush assessment of trends in time, our understanding of jaguar conservation status in the NRU, and other significant, large areas across the jaguar's range, will be better when the results of occupancy monitoring are complemented by a more complete understanding of population parameters that require individual identification. We can accomplish this through select, long-term research sites set in the larger conservation landscape matrix.

Large occupancy surveys provide unbiased guidance in where to conduct long-term monitoring of trends in abundance that tells us if populations are increasing, decreasing, or remaining stable. In these focal areas, trends in the density of jaguars can be rigorously measured through photographic and genetic capture-recapture methods, following the detailed guidance provided in our [Abundance and Density](#) section. Across jaguar range, when using camera traps for density estimates we specifically recommend numerous units, ample spacing of stations, and large sample areas. For the NRU we recommend a minimum of 60 camera trap stations, all spaced approximately 4 km from each other, to sample approximately 960 km². Our recommendations include procedures for data collection at each station to examine covariates, data storage and analyses. Data should be analyzed using spatially explicit capture-recapture (SCR) models, but we also recommend conventional non-SCR models when assessing trends. Repeated non-SCR surveys assessed as single season closed population estimates, and again across multiple years, will provide estimates of time specific abundance, annual survival, and number of new recruits. Methods for assessing trends using SCR methods should be advanced and tested. Multi-year scat surveys for genetic CR are an alternative and/or complementary method of capture-recapture sampling. We recommend using scat dogs for efficient sampling in large sections of the NRU, and provide guidance on how to sample large areas to allow all resident females an equal probability of being captured through scats. These recommendations on how to conduct genetic capture-recapture sampling in the NRU have application anywhere in jaguar range.

[Population Genetics](#) methods are powerful tools to reveal otherwise elusive large scale and long-term details of movements, relatedness, and population status. Occupancy sampling can ensure productive searches with scat dogs that are guided by confidence of where jaguars are most

likely to be. We recommend using the mtDNA cytochrome b gene for its versatility; it can be used to separate jaguars and pumas, and also identify other carnivores.

Occupancy surveys can locate the best areas for long-term in depth research, but those sites should also be selected because of their potential to be defended through time, and their potential role as population sources. Detailed studies require secure study areas where trends and individual animals can be followed for years.

In these focal areas telemetry, genetic studies, and camera trapping can clarify [Demographic Parameters and Spatial Ecology](#). We need to know more about jaguar movements across complex landscapes, and we need a better understanding of the characteristics of dispersal and long range movements. Population losses and gains can be tracked using camera traps and/or telemetry. However, for either method, only a long-term commitment will result in enough data to generate meaningful results. Survival studies, in particular, require abundant data, across many years.

GPS telemetry has expanded our ability to understand how jaguars use space, but the technological advances need to be matched by well-designed hypotheses and ancillary data that provides context for jaguar movements. We recommend the use of home-range estimators based on utilization distributions and present options for defining jaguar habitat. When designing [habitat selection](#) studies, assessments of resources should be on the same temporal-spatial scale as radio-location data, and attempt similar resolution for meaningful analyses.

All the above approaches function in complementary ways to build a deep understanding of jaguar population ecology, and clarify the threats, trends, and the biological factors that determine the status of a jaguar population and increases its connectivity with neighboring areas.

Jaguar conservation across the NRU and range wide will benefit from better coordination and curation of data. Building on the experience gained in the NRU and collectively in study areas across the jaguar's range we offer a system of [Data Curation](#), which will allow efficient assessments of the jaguar's status throughout the NRU, with the potential to be expanded range wide.

Carnivore conservation is accomplished by mitigating a suite of threats. As examples, the factors reducing wolf survival in the Northern Rockies are human caused mortality, but this can be related to the percent of home ranges including agricultural land/livestock versus core protected areas with natural prey (Smith et al. 2010). Grizzly bear survival is best explained by degree of human development and road density (Schwartz et al. 2010). Amur tiger home ranges focus on the location of their ungulate prey (Hojnowski et al. 2012). Jaguars can survive in area dominated by ranchlands, but only if large areas of habitat for jaguars and prey are set aside, apart from the cattle operations (Polisar et al. 2003, Azevedo and Murray 2007a, b, Cavalcanti and Gese 2009, 2010, Hoogesteijn and Hoogesteijn 2011). As large jaguar source areas become increasingly disjunct from each other, indirect and direct threats require concrete conservation

mechanisms – whether they are incentives or enforcement or their complementary combination – for corridors to function.

In northern Mexico and the United States, jaguars are on the edge, of their range. Between every large jaguar conservation unit, jaguars are on the edge. As time passes and pressures mount across the jaguar's range (e.g., hydrocarbon extraction, roads, reservoirs, agricultural crops, urban expansion, and direct killing of jaguars), jaguars are increasingly on the edge. What is the status of jaguars range wide? Are they increasing, decreasing, or stable? This protocol proposes cost-effective sampling methods for an extremely large area (>200,000km²) as an example of what can be used for a rigorous, field-sampling-based range-wide assessment. It presents guidance for more detailed studies on demographic patterns, and studies that elucidate how jaguars move across the landscape and select habitats. Knowing where your study animal is paramount. Understanding its status is critical. Comprehending how jaguars make a living, knowing which environmental parameters lead to their survival and increase, and providing those factors in abundance is essential to effect jaguar conservation range wide.

Humans still need expansive wild places with big scary mammals that challenge us. By conserving those life forms in their wild environments, we benefit our own survival. If we accomplish that, then we will prove that we have earned our self-given name – sapiens – the wise.

We agree with that statement made by Logan and Sweanor (2001). It is our hope that this monitoring document helps hold ground for jaguars, and provides additional kindling for the jaguar's wild spirit to repopulate places where the fire has temporarily been extinguished.

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Table 1. The Northwestern Recovery Unit (NRU) by components.

NRU Components	Total Area ^a km ²	Suitable Habitat ^b km ²	Core Habitat ^c km ²
Borderlands Secondary Area – US Portion	29,021	6,682	0.0
Borderlands Secondary Area – Mexico Portion	33,955	22,915	431
Sonora Core Area	77,710	67,889	28,294
Sinaloa Secondary Area	31,191	28,753	18,847
Jalisco Core Area/Sinaloa sub- population	59,949	44,404	26,315

^aTotal areal estimates extracted from Sanderson and Fisher (2013).

^b“Suitable Habitat” estimates represent the area with a suitability index greater than zero, based on tree cover, terrain roughness, distance to water, human influence, and ecoregions (Sanderson and Fisher 2013).

^c“Core Habitat” estimates represent all suitable habitat that has a modeled jaguar density (based on the relationship of habitat suitability model with observed densities across the NRU) greater than or equal to 1 jaguar per 100 km² that has contiguous blocks of area capable of supporting 3 or more females (Sanderson and Fisher 2013).

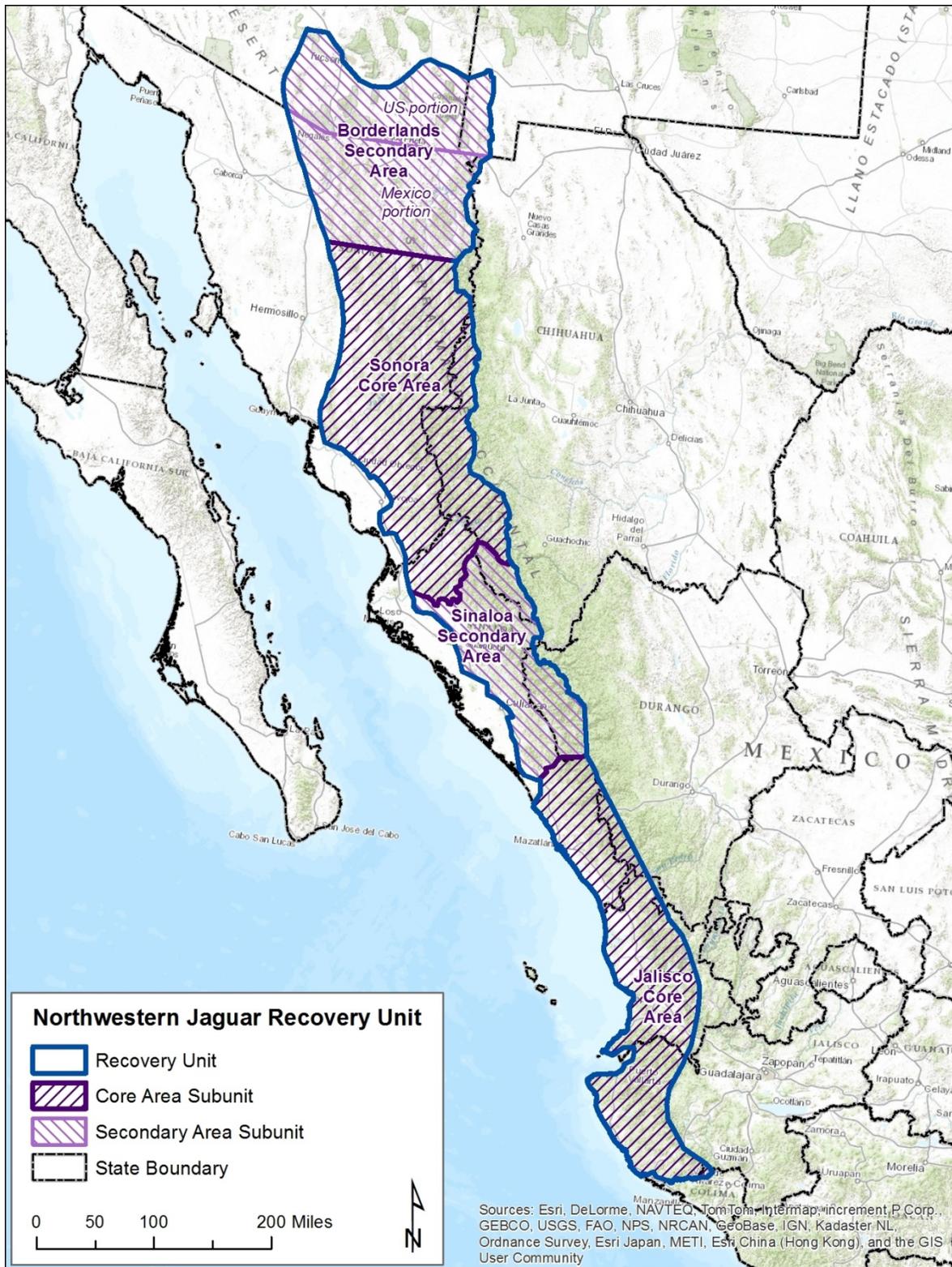


Figure 1. The 226,826 km² Northwestern Jaguar Recovery Unit (NRU) straddles the United States-Mexico border with approximately 29,021 km² in the United States and 197,805 km² in Mexico.

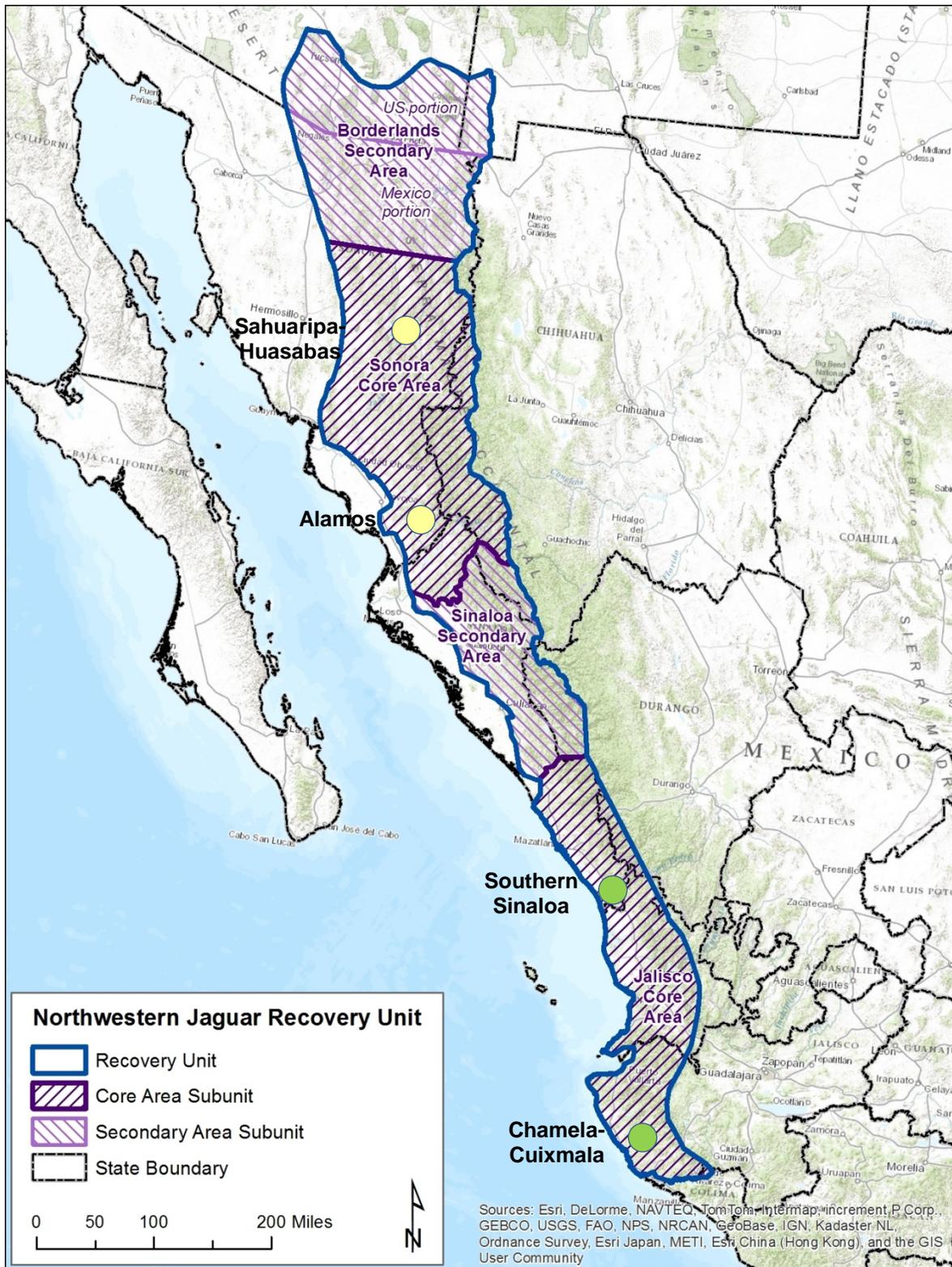


Figure 2. Known breeding populations in the Sonora Core Area occur in Sahuaripa-Huasabas and Alamos (yellow dots), and in the Jalisco Core Area occur in southern Sinaloa and Chamela-Cuixmala (green dots).

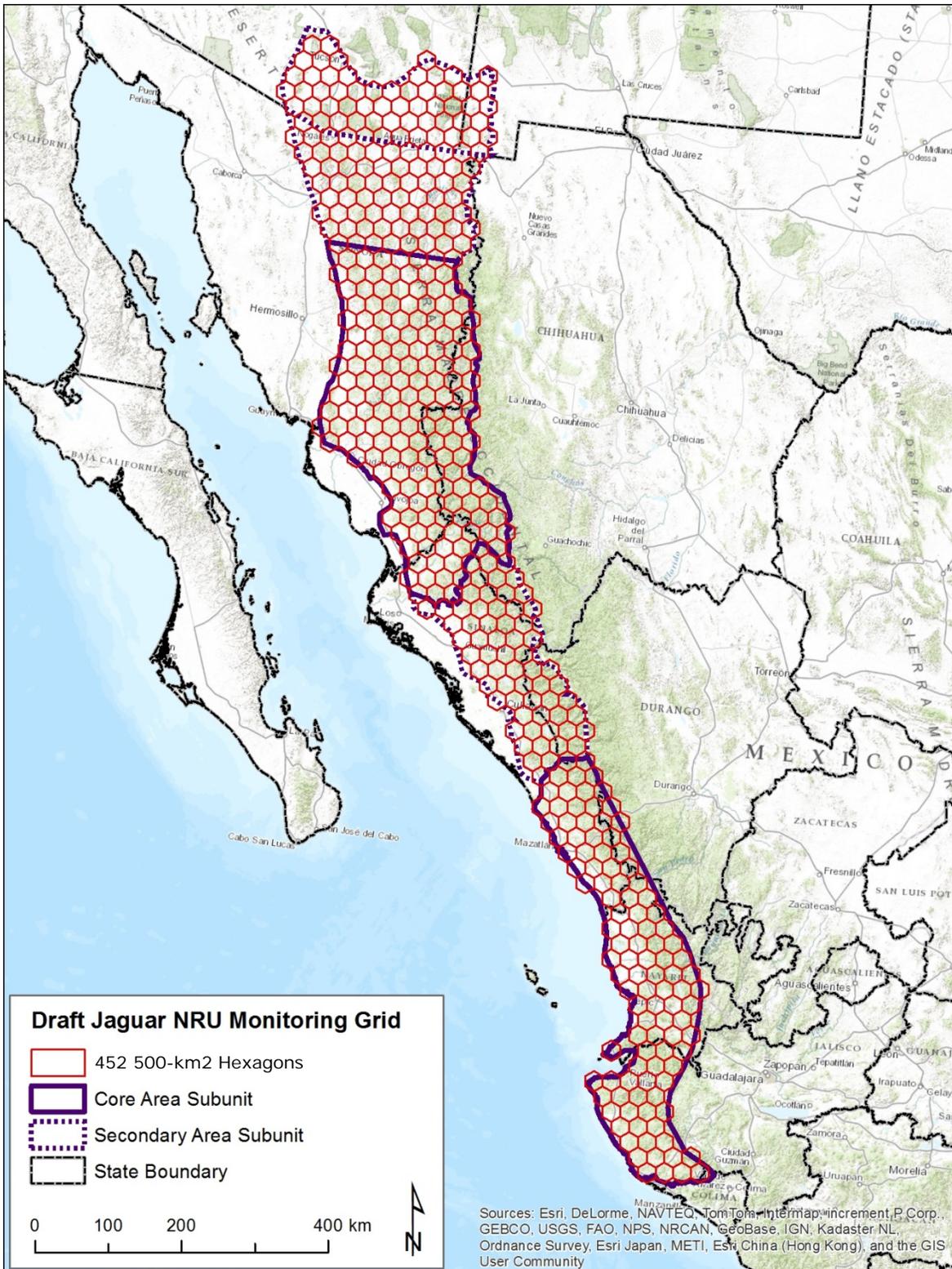


Figure 3. A grid of 452 500-km² hexagons across the 226,826 km² Northwestern Jaguar Recovery Unit (NRU).

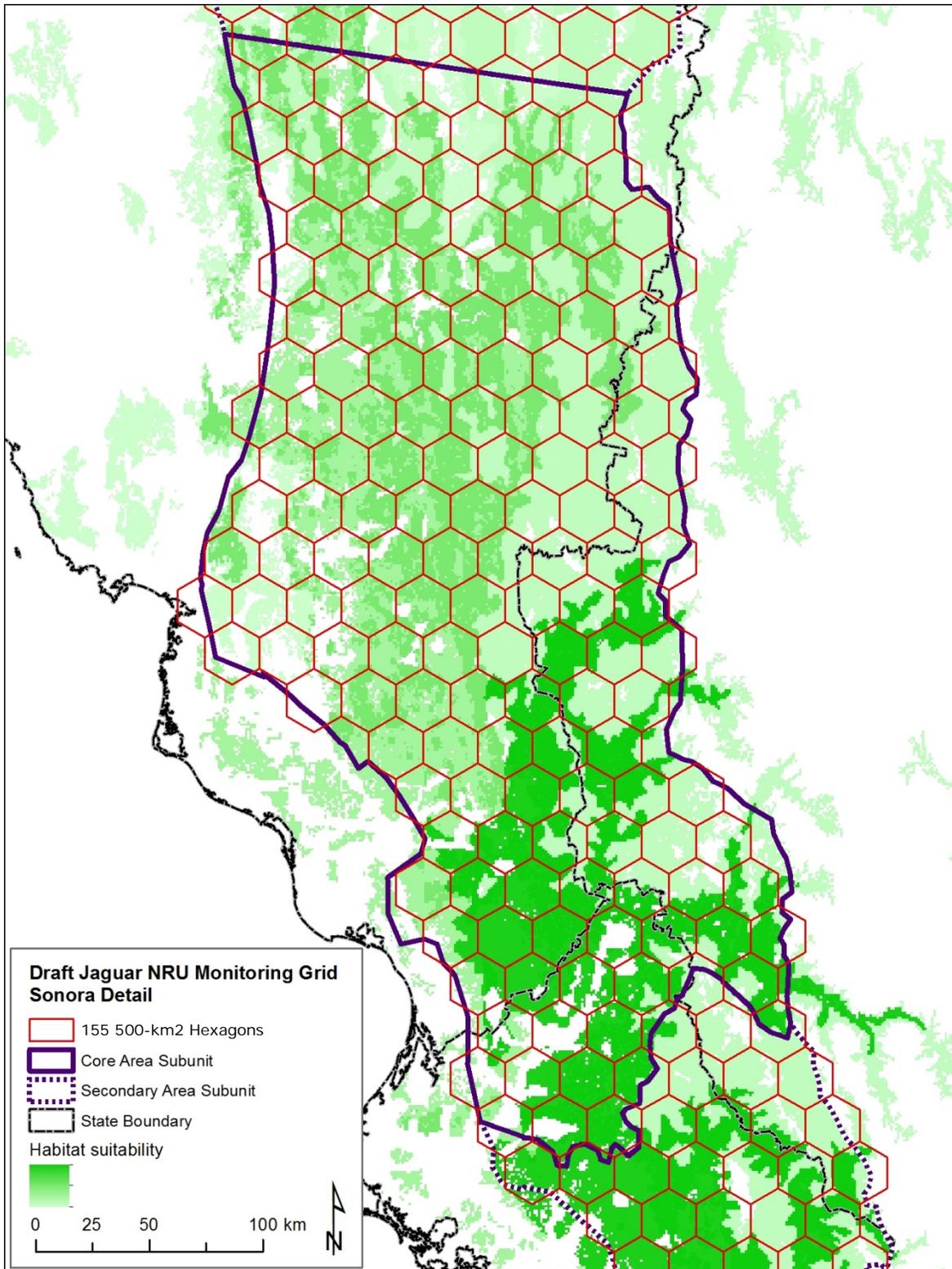


Figure 4. A grid of 155 500-km² hexagons across the 77,710 km² Sonora Core Area in northern Mexico. Habitat suitability index at 1-km² resolution, darker shades of green indicating higher suitability (Sanderson and Fisher 2013).

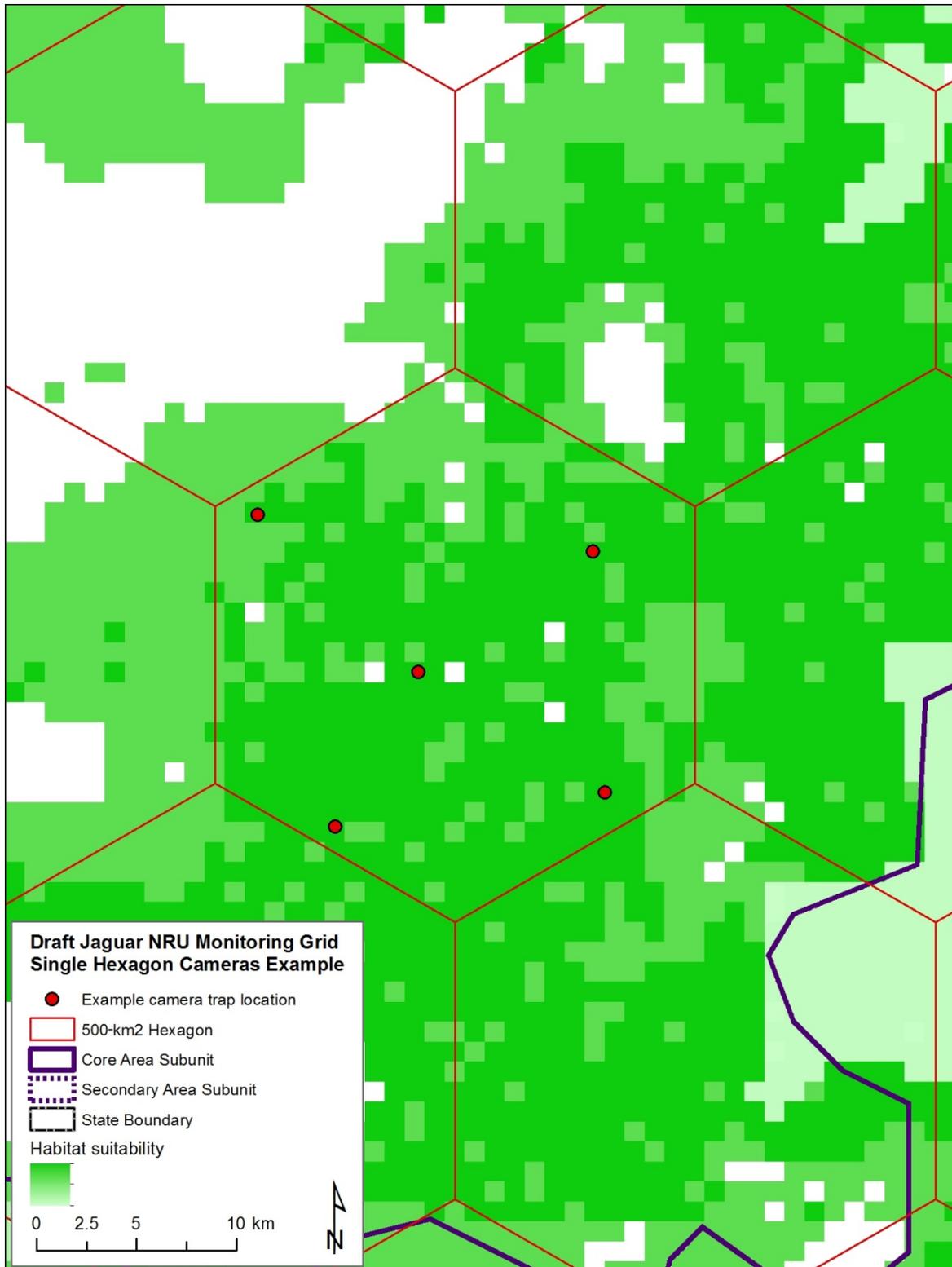


Figure 5. Individual camera-trap locations within a 500-km² hexagon in the 77,710 km² Sonora Core Area in northern Mexico. Habitat suitability index at 1-km² resolution, darker shades of green indicating higher suitability (Sanderson and Fisher 2013).

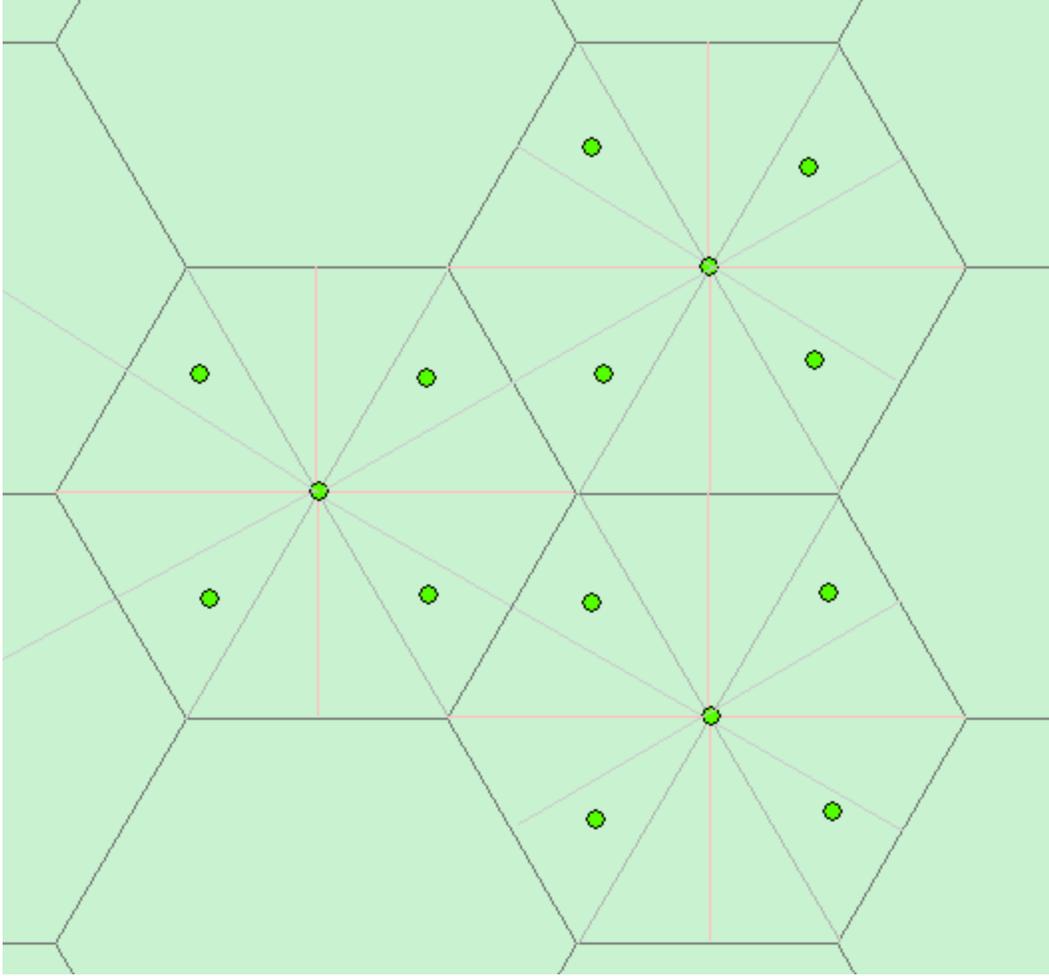


Figure 6. Possible within-hexagon camera-trap setup maximizing spatial coverage.



Figure 7. Guido Ayala and Maria Vizcarra testing 2 camera traps set on opposite sides of a trail in Bolivia. Photo by Julie Maher.



Figure 8. Camera trap sampling using paired cameras in the Upper Caura watershed, Guianan Shield Forests, Venezuela. Photo by Lucy Perera.

record_id	lat	long	date_year	date_month	date_day	date_time	identity_type	lifestage_type	sex_type

Figure 9. A standard template for the table in either csv or xls format is in the process of being specified, provisionally with the columns above.

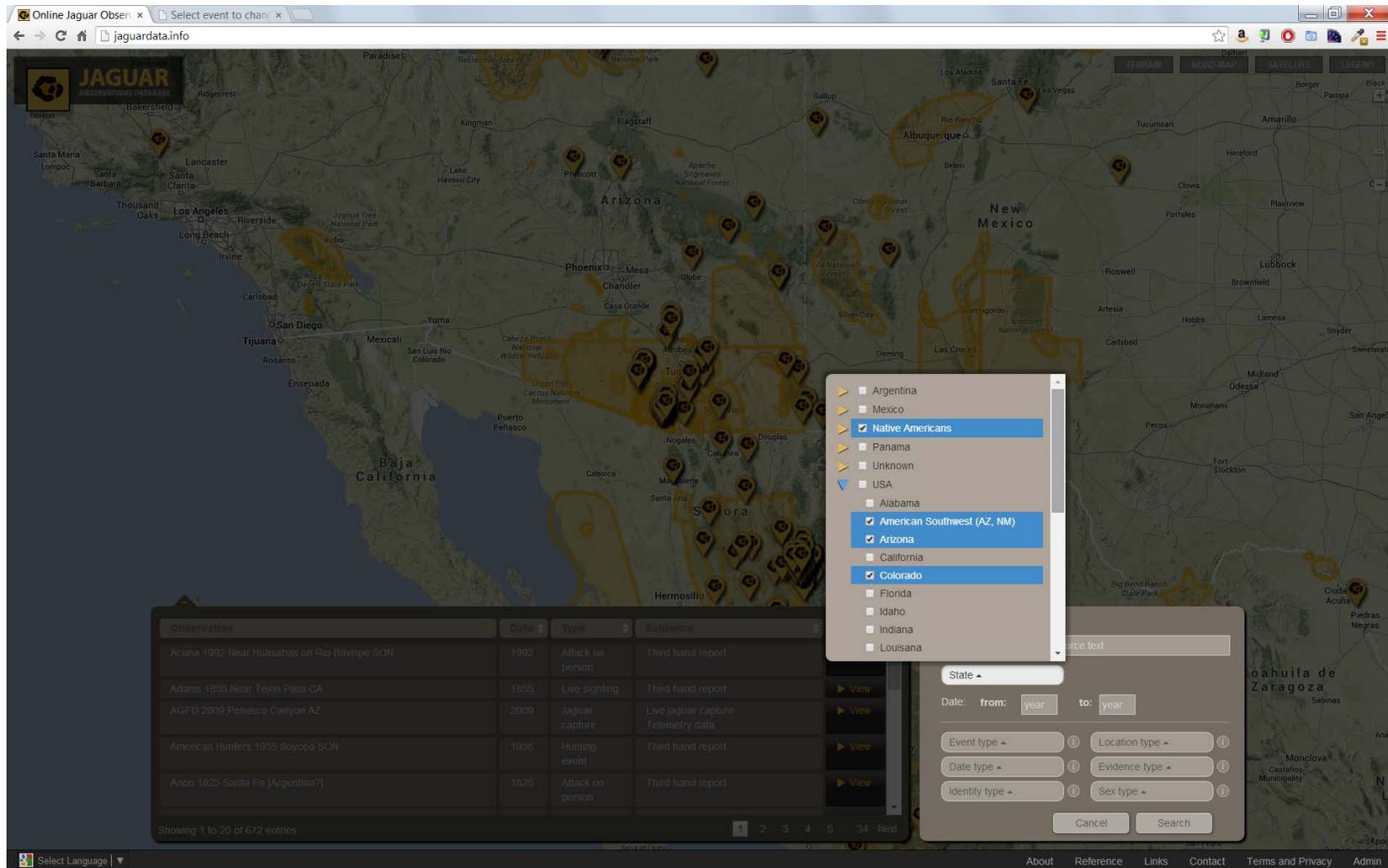


Figure 10. Public interface to jaguar observation database (<http://jaguardata.info/>) developed by the Wildlife Conservation Society, showing controls that allow the user to filter by text, geographic location, year, event type, specificity of location and date, evidence type, and individual identity and sex.

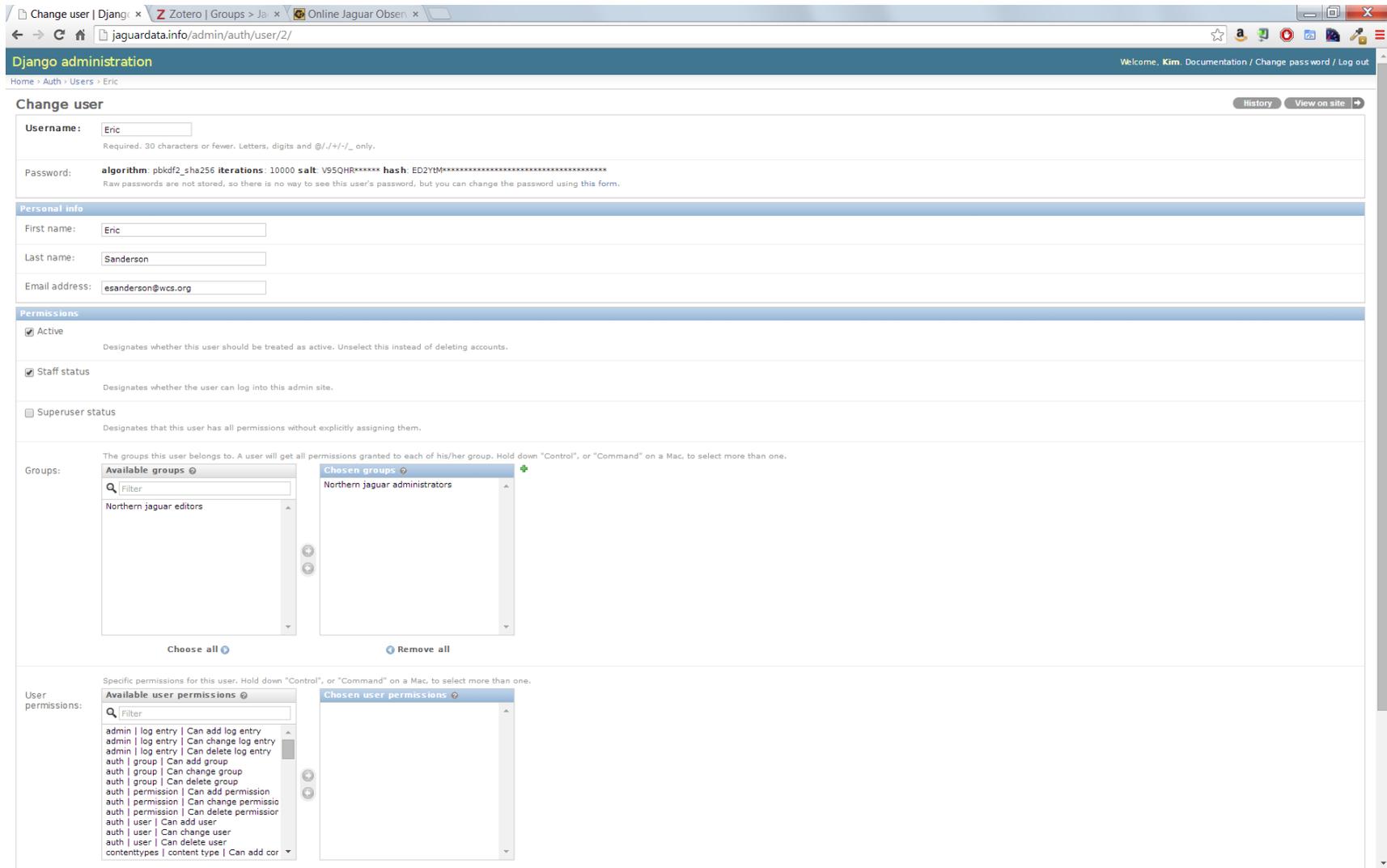


Figure 11. User administration interface of the jaguar observation database (<http://jaguardata.info/>) developed by the Wildlife Conservation Society.

Select event to change

Search

Action: 0 of 100 selected

ID	Name	Point	Record area	Locality type	State	Event type	Individuals	Evidence types	Year	Date type	Accessid
360	Lee 1950 Rio Yaqui SON	(None)	(None)	Defined Area	Sonora	Hunting event	Jaguar Male [Jaguar Male - certain Adult - assumed]	First hand report	1950	Few Years	114
361	Lee 1964 West Coast of Mexico	(None)	(None)	Wide Area	Sinaloa	Attack on person	Jaguar [Jaguar Unknown or unattributed Unknown or unattributed]	Third hand report	1964	Prior to a given year	492
363	Leopold 1922 Delta of Colorado River AZ	(None)	Delta of the Colorado River (neighborhood)	Defined Area	Arizona	Scientific study	No jaguar [Absence Not applicable Not applicable]	First hand report	1922	Year	351
100	Leopold 1955 San Pedro Martir BCN	(None)	(None)	Defined Area	Baja California Norte	Hunting event	Jaguar Male [Jaguar Male - certain Adult - assumed]	Hide	1955	Month-Year	421
101	Leopold 1959 San Ignacio SIN	(None)	(None)	Defined Area	Sinaloa	Unknown	Jaguar [Jaguar Unknown or unattributed Unknown or unattributed]	Third hand report	1959	Prior to a given year	297
102	Leopold 1959 Santiago SIN	(None)	(None)	Defined Area	Sinaloa	Hunting event	Jaguar Male [Jaguar Male - certain Adult - assumed]	Third hand report	1959	Prior to a given year	296
364	Lilly 1909 Dog Springs NM	POINT (-108.762730000000000048 31.3399430000000000017)	(None)	Determined Point	New Mexico	Hunting event	Jaguar [Jaguar Unknown or unattributed Unknown or unattributed]	Third hand report	1909	Year	45
365	Lilly 1950 Arizona and New Mexico	(None)	Arizona and New Mexico (state)	Very Wide Area	American Southwest (AZ, NM)	General observation	No jaguar [Absence Not applicable Not applicable]	Unknown or unattributed	1950	Nearest Century	979
125	Lion Hunter 1989 Arizpe SON	POINT (-109.938738999999999982 30.3595219999999999983)	(None)	Determined Point	Sonora	Hunting event	Jaguar [Jaguar Unknown or unattributed Unknown or unattributed]	Third hand report	1989	Year	101
149	Lion Hunter 1994 Rancho Los Taraiques SON	POINT (-110.582742999999999936 29.6678970000000000004)	(None)	Determined Point	Sonora	Hunting event	Jaguar Male [Jaguar Male - certain Adult - assumed]	Second hand report	1994	Year	92
150	Lion Hunter 1994 Rancho San Vicente SON	POINT (-109.050200000000000038 27.4961650000000000013)	(None)	Determined Point	Sonora	Killed after predation	Jaguar Male [Jaguar Male - certain Adult - assumed]	Photograph or video Second hand report	1994	Year	93
165	Lion Hunter 1997 Rancho La Poza SON	(None)	(None)	Determined Point	Sonora	Killed after predation	Jaguar Female [Jaguar Female - certain Adult - assumed]	Photograph or video Second hand report	1997	Year	80
177	Lion Hunter 1998 Rancho Los Pescador SON	POINT (-109.052406000000000048 29.5897250000000000014)	(None)	Determined Point	Sonora	Killed after predation	Jaguar cub [Jaguar Unknown or unattributed Cub - certain] Jaguar Female [Jaguar Female - certain Adult - assumed]	Second hand report	1998	Month-Year	74
116	Local people 1980 Los Angeles Ranch SIN	POINT (-105.8038999999999999987 22.6656000000000000013)	(None)	Defined Point	Sinaloa	Skin or skull seen	Jaguar [Jaguar Unknown or unattributed Unknown or unattributed]	Second hand report	1980	Decade	291
128	Local People 1990 Baroten SIN	POINT (-108.598600000000000047 26.3958000000000000013)	(None)	Defined Point	Sinaloa	Hunting event	Jaguar [Jaguar Unknown or unattributed Unknown or unattributed]	Third hand report	1990	Year	289
366	Lopez 1991 Coronado National Monument AZ	(None)	Coronado National Monument (mountain range)	Defined Area	Arizona	Live sighting	Jaguar [Jaguar Unknown or unattributed Unknown or unattributed]	Third hand report	1991	Year	204
375	Lopez-Gonzalez 1999-2012 Northern Jaguar Reserve 100 SON	POINT (-109.1883260000000000035 29.4653260000000000010)	(None)	Defined Point	Sonora	Scientific study	Jaguar [Jaguar Unknown or unattributed Unknown or unattributed]	Photograph or video	2012	Decade	878
378	Lopez-Gonzalez 1999-2012 Northern Jaguar Reserve 10 SON	POINT (-109.1240370000000000013 29.4167039999999999993)	(None)	Defined Point	Sonora	Scientific study	Jaguar [Jaguar Unknown or unattributed Unknown or unattributed]	Photograph or video	2012	Decade	788
377	Lopez-Gonzalez 1999-2012 Northern Jaguar Reserve 11 SON	POINT (-109.0974290000000000053 29.3285429999999999998)	(None)	Defined Point	Sonora	Scientific study	Jaguar [Jaguar Unknown or unattributed Unknown or unattributed]	Photograph or video	2012	Decade	789
376	Lopez-Gonzalez 1999-2012 Northern Jaguar Reserve 12 SON	POINT (-109.081290999999999931 29.3869420000000000012)	(None)	Defined Point	Sonora	Scientific study	Jaguar [Jaguar Unknown or unattributed Unknown or unattributed]	Photograph or video	2012	Decade	790
374	Lopez-Gonzalez 1999-2012 Northern Jaguar Reserve 13 SON	POINT (-109.2086070000000000007 29.5063749999999999985)	(None)	Defined Point	Sonora	Scientific study	Jaguar [Jaguar Unknown or unattributed Unknown or unattributed]	Photograph or video	2012	Decade	791
373	Lopez-Gonzalez 1999-2012 Northern Jaguar Reserve 14 SON	POINT (-109.1115319999999999969 29.3617039999999999996)	(None)	Defined Point	Sonora	Scientific study	Jaguar [Jaguar Unknown or unattributed Unknown or unattributed]	Photograph or video	2012	Decade	792
372	Lopez-Gonzalez 1999-2012 Northern Jaguar Reserve 15 SON	POINT (-109.1970050000000000043 29.4783189999999999991)	(None)	Defined Point	Sonora	Scientific study	Jaguar [Jaguar Unknown or unattributed Unknown or unattributed]	Photograph or video	2012	Decade	793
371	Lopez-Gonzalez 1999-2012 Northern Jaguar Reserve 16 SON	POINT (-109.1992419999999999981 29.4877070000000000003)	(None)	Defined Point	Sonora	Scientific study	Jaguar [Jaguar Unknown or unattributed Unknown or unattributed]	Photograph or video	2012	Decade	794
370	Lopez-Gonzalez 1999-2012 Northern Jaguar Reserve 17 SON	POINT (-109.1848099999999999934 29.4771719999999999995)	(None)	Defined Point	Sonora	Scientific study	Jaguar [Jaguar Unknown or unattributed Unknown or unattributed]	Photograph or video	2012	Decade	795
369	Lopez-Gonzalez 1999-2012 Northern Jaguar Reserve 18 SON	POINT (-109.1780880000000000025 29.4228239999999999990)	(None)	Defined Point	Sonora	Scientific study	Jaguar [Jaguar Unknown or unattributed Unknown or unattributed]	Photograph or video	2012	Decade	796
368	Lopez-Gonzalez 1999-2012 Northern Jaguar Reserve 19 SON	POINT (-109.3137000000000000045 29.4228239999999999990)	(None)	Defined Point	Sonora	Scientific study	Jaguar [Jaguar Unknown or unattributed Unknown or unattributed]	Photograph or video	2012	Decade	797

Figure 12. Jaguar event listing of the jaguar observation database (<http://jaguardata.info/>) developed by the Wildlife Conservation Society.

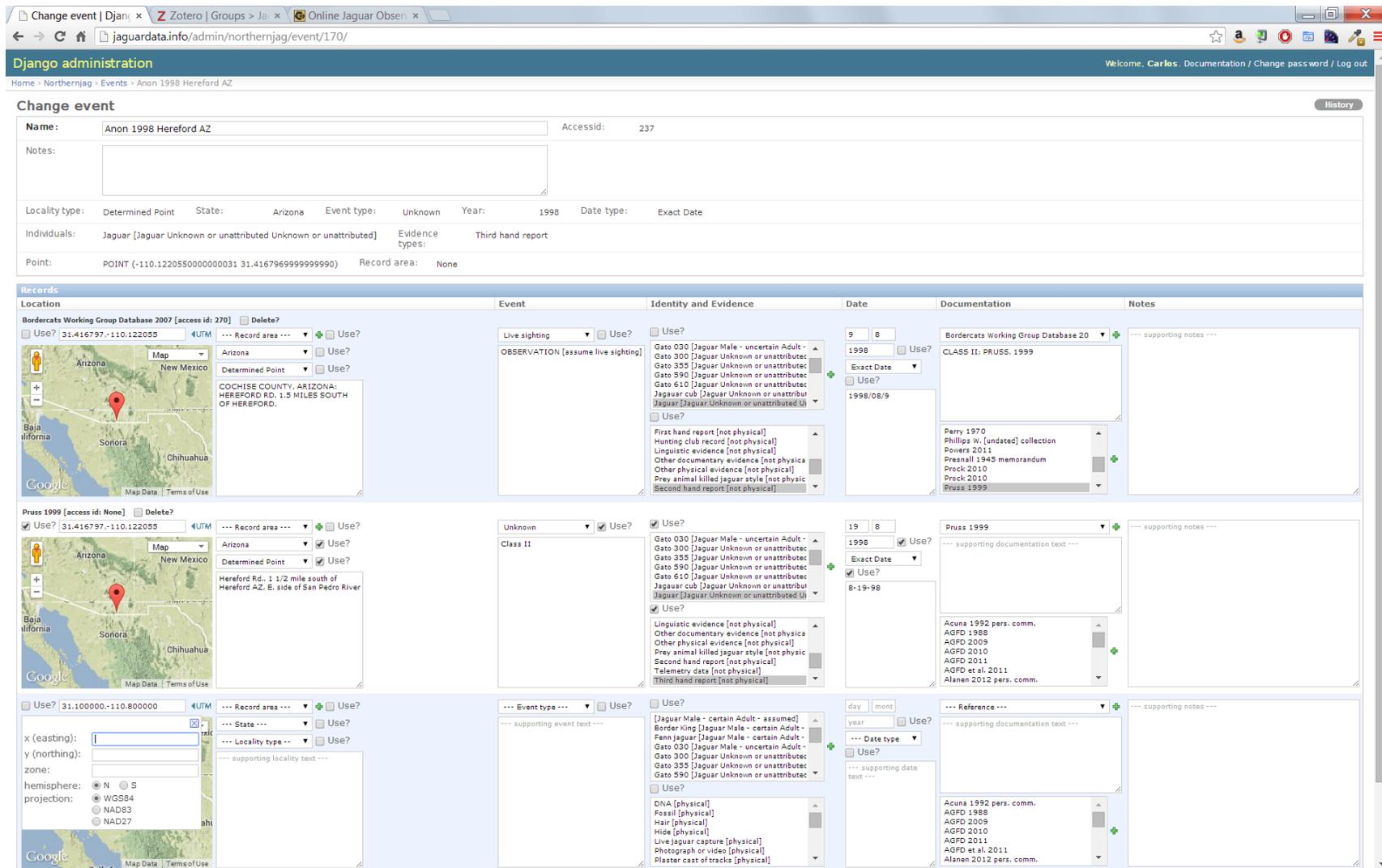


Figure 13. Event editing interface of the jaguar observation database (<http://jaguardata.info/>) developed by the Wildlife Conservation Society.

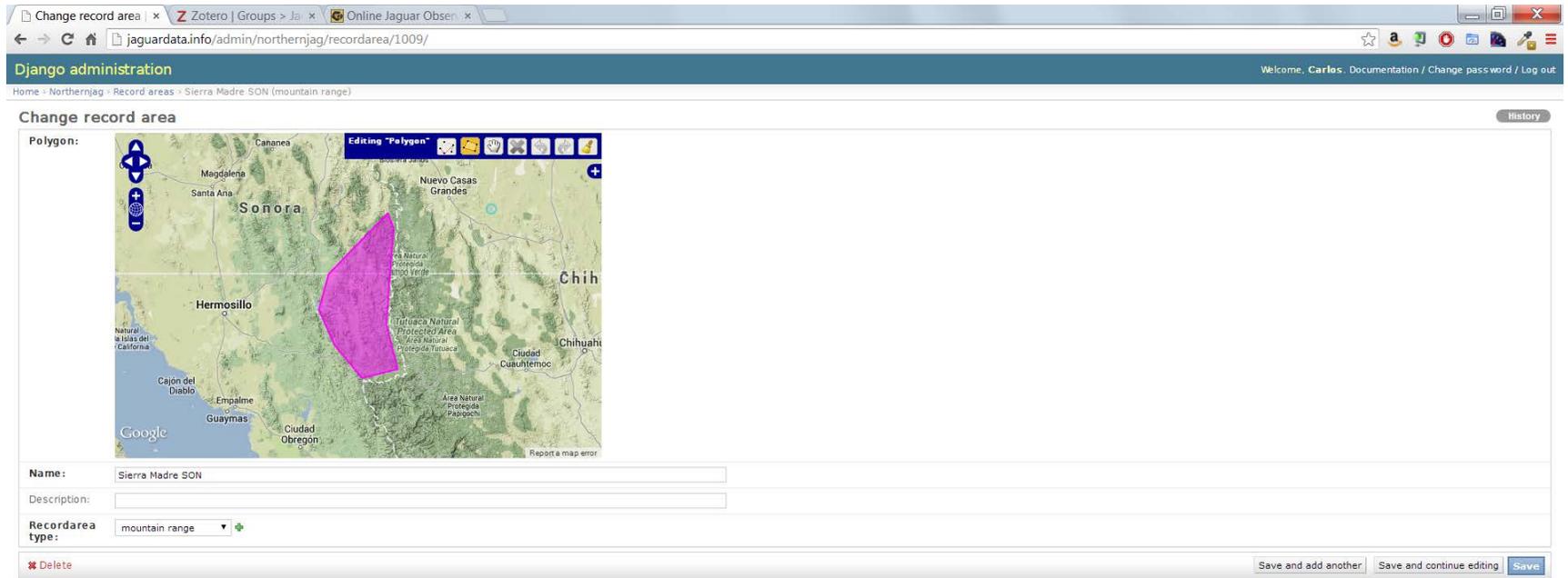


Figure 14. Editing a polygonal record area for association with non-point jaguar events of the jaguar observation database (<http://jaguardata.info/>) developed by the Wildlife Conservation Society.

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https://www.zotero.org/groups/jaguars_in_the_southwest/items

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Title	Creator	Date Modified
2011 - New record of the European jaguar, Panthera onca gomb...	Logchem	5/2/2014 4:18 PM
A Fauna from an Indian Site near Redington, Arizona	Burt	6/2/2014 9:45 AM
A Jaguar in Texas	Anonymous	2/7/2011 12:30 PM
A jaguar was caught in Arizona	Barnett	2/7/2011 12:30 PM
A long-term perspective on woody plant encroachment in the d...	Brunelle et al.	5/5/2014 1:24 PM
A narrative of the captivity and suffering of Dolly Webster ...	Dolbear	6/2/2014 12:35 PM
A possible occurrence of the jaguar in Louisiana	Nowak	2/7/2011 12:30 PM
A Reevaluation of the Harrodsburg Crevice Fauna (Late Pleist...	Smith and Polly	5/24/2014 8:34 AM
A Rock Art Inventory at Hueco Tanks State Park, Texas	Davis and Jones	6/2/2014 12:16 PM
A spatial model of potential jaguar habitat in Arizona	Hatten et al.	11/15/2010 4:05 PM
A spatial model of potential jaguar habitat in Arizona	Hatten et al.	2/7/2011 12:30 PM
A Survey of North American Indian Rock Art	Wellman	6/2/2014 12:20 PM
A synthetic review of feedbacks and drivers of shrub encroac...	D'Odorico et al.	5/5/2014 1:28 PM
Aboriginal pottery of eastern United States	Holmes	6/10/2014 2:20 PM
Agency: Mine would stress, but not kill, jaguar	Davis	5/4/2014 4:46 PM
AGFD HDMS shapefile for jaguars	Alanen	6/2/2014 4:21 AM
[AGFD Report on Fenn Jaguar observation 2011 - 11 - 19]	Miller	8/24/2012 2:09 PM
Alianza para conservar al jaguar en el suroeste de Estados U...	van Pelt and Johnson	3/18/2014 4:56 PM
All Souls' Procession and Macho B Memorial	Center for Biological Diversity	5/4/2014 5:53 PM
Ambushed on the Jaguar Trail	Childs and Childs	5/26/2014 9:08 AM
An ethnologic dictionary of the Navaho language	Franciscan Fathers of the Navajo	6/2/2014 1:27 PM
An Indomitable Beast: The Remarkable Journey of the Jaguar, ...		5/7/2014 12:35 PM
Anasazi Mural Art of the Pueblo IV Period, A.D. 1300 - 1600:...	Crotty	6/2/2014 10:31 AM
ANOMALOUS FELIDS (Dorsal jaguar)	Hartwell	5/4/2014 9:38 PM
Apache Dictionary	Uplegger	5/7/2014 3:56 PM

1 to 25 of 347

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Figure 15. Zotero jaguar bibliography linked to the jaguar observation database (<http://jaguardata.info/>) developed by the Wildlife Conservation Society.

APPENDIX 1: GLOSSARY

Área de Protección de Flora y Fauna Silvestre (APFF): areas of Mexico established in accordance with the general provisions of the Ecology Law and other applicable laws in areas containing habitats whose existence depend preservation, transformation and development of species of wild flora and fauna. In October 2013 there were 37 areas, protecting 66,872 km², representing 3.4% of the national territory.

Área de Protección de Recursos Naturales (APRN): areas of Mexico designated for preservation and protection of the soil , watersheds , water and natural resources generally located on forest land suitability for forestry.

Áreas Naturales Protegidas (ANP): areas of Mexico over which the nation exercises sovereignty and jurisdiction where the original environments have not been significantly altered by human activity or require to be preserved and restored. They are created by presidential decree and activities that can be performed on them are established in accordance with the General Law of Ecological Balance and Environmental Protection, Regulations, program management and ecological management programs. They are subject to special protection, conservation, restoration and development, according to categories established by the Act. The National Commission of Natural Protected Areas currently manages 176 natural areas of federal character representing more than 253,948 km². ANPs may contain some federally owned lands, but generally land-ownership within ANPs is either private or ejido lands. See <http://www.conanp.gob.mx/regionales/>

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.

Biosphere Reserve (UNESCO): Biosphere reserves are sites established by countries and recognized under UNESCO's Man and the Biosphere (MAB) Programme to promote sustainable development based on local community efforts and sound science. As places that seek to reconcile conservation of biological and cultural diversity and economic and social development through partnerships between people and nature, they are ideal to test and demonstrate innovative approaches to sustainable development from local to international scales. See <http://www.unesco.org/new/en/natural-sciences/environment/ecological-sciences/biosphere-reserves/>

Biosphere Reserve (Sonora): The geologically unique El Pinacate y Gran Desierto de Altar Biosphere Reserve in Sonora is adjacent to the Cabeza Prieta National Wildlife Refuge and the Organ Pipe Cactus National Monument/Biosphere Reserve in the United States, thus forming an extensive, even if primarily arid land, protected area complex spanning the international Mexico-USA border.

Convergence: a condition in statistical modeling when the iterative process used to estimate model coefficients was unable to find appropriate solutions, indicating that the coefficients are not meaningful.

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.

Core habitat (Sanderson and Fisher 2013): is all suitable habitat that has a modeled jaguar density (based on the relationship of the habitat suitability model with observed densities across the NRU) greater than or equal to 1 per 100 km², and has contiguous blocks of area capable of supporting 3 or more females.

Corridor: area connecting protected areas/source sites.

Critical habitat: is a specific geographic area(s) that contains features essential for the conservation of a threatened or endangered species and that may require special management and protection. Critical habitat may include an area that is not currently occupied by the species but that will be needed for its recovery.

Ejido: is an area of communal land used for agriculture, on which community members individually possess and farm a specific parcel. Ejidos are registered with Mexico's National Agrarian Registry (Registro Agrario Nacional).

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.

Nuisance parameter: any parameter or variable which is not of immediate interest but which must be accounted for in the analysis of those parameters which are of interest. The classic example of a nuisance parameter is the variance, σ^2 , of a normal distribution, when the mean, μ , is of primary interest.

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.

Primary occasion: a duration of sampling, usually seasons or years, and subdivided into repeat visits to sample sites – so-called secondary occasions.

Primero Conservation: non-profit organization created to work with counterparts in Sonora to mitigate killing of carnivores and monitor fauna on cattle ranches near the confluence of the Aros and Bavispe Rivers (Moreno et al. 2013).

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.

Ramsar Site: a wetland of international importance under The Convention on Wetlands (Ramsar, Iran, 1971), called the "Ramsar Convention". The Convention is an intergovernmental treaty that embodies the commitments of its member countries to maintain the ecological character of their Wetlands of International Importance and to plan for the "wise use", or sustainable use, of all of the wetlands in their territories. See http://www.ramsar.org/cda/en/ramsar-cop12-logo-homeindex/main/ramsar/1%5E26530_4000_0 and http://www.ramsar.org/cda/en/ramsar-news-2rs-mexico/main/ramsar/1-26%5E25013_4000_0

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.

State variables: variables that are used to quantify the current status of a community or population, including species richness (number of species), occupancy (proportion of an area occupied by a species or fraction of landscape units where the species is present), and density (number of individuals per unit area).

Suitable habitat: the area with a suitability index greater than 0, based on tree cover, terrain roughness, distance to water, human influence, and ecoregions (Sanderson and Fisher 2013).

Terrestrial conservation priority area: the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (National Commission for the Knowledge and Use of Biodiversity; CONABIO) has conducted gap analyses to identify priority areas for conservation. In the most recent review, experts combined high resolution species distribution modeling and maps, with weighted threats to biodiversity to generate maps of ranked terrestrial priority sites for conservation. There are a substantial number and area of high and extreme priority sites for conservation in the Mexico portion of the NRU (Urquiza-Hass et al. 2009).

Unidad de Manejo para la Conservación de Vida Silvestre (UMA): Management units under any ownership (private, ejido, communal, federal, etc.) established to help harmonize and mutually strengthen biodiversity conservation with the needs of production and socio-economic development in rural areas of Mexico. See <http://www.semarnat.gob.mx/temas/gestion-ambiental/vida-silvestre/sistema-de-unidades-de-manejo> and http://app1.semarnat.gob.mx/dgeia/informe_04/05_aprovechamiento/recuadros/c_rec1_05.htm

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.

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**APPENDIX 2:
APRIL 2014 WORKSHOP PARTICIPANTS**

Jaguar quantitative sampling and monitoring scientists and agency personnel contributing to the development of a jaguar survey and monitoring protocol at a workshop hosted by the Wildlife Conservation Society (WCS) in April, 2014, at the Ladder Ranch in Caballo, New Mexico.

<u>Name</u>	<u>Title, Institution, and Location</u>	<u>Area of Expertise</u>
Marit Alanen	Fish and Wildlife Biologist, U.S. Fish and Wildlife Service (USFWS), Tucson, Arizona	USFWS Project Manager
Carlos De Angelo	National Research Council, Instituto de Biología Subtropical, Universidad Nacional de Misiones, Puerto Iguazu, Argentina	Jaguars in Argentina, ecology and conservation, methods for large scale public monitoring of jaguars
Fernando C.C. Azevedo	Professor, Departamento de Ciências Naturais, Universidade Federal de São João del Rei, Brazil/Pantanal/Iguaçu	Jaguars in Brazil, ecology and conservation, human-jaguar coexistence
Jon Beckmann	Conservation Scientist/North America Connectivity Coordinator, Wildlife Conservation Society, Bozeman, Montana	Large carnivore ecology and connectivity, genetic and telemetry field sampling for population analyses
Melanie Culver	Assistant Professor, Wildlife and Fisheries Science, University of Arizona, Arizona Cooperative Wildlife Research Unit, Tucson	Jaguars in the southwestern U.S., application of population genetics to field programs
Kim Fisher	GIS Programmer, Wildlife Conservation Society, Bronx, New York	Jaguar habitat modeling throughout the NRU
Carlos López-González	Co-leader Jaguar Recovery Team/University of Querétaro, Mexico/Sonora	Jaguars in Sonora and Mexico, ecology and history of borderlands jaguars

Bart Harmsen	Fellow Wildlife Chair, Environmental Research Institute, University of Belize, Belmopan, Belize/Panthera/Belize/Mesoamerica	Jaguars in Belize, population estimation methods
Marcella Kelly	Associate Professor, Department of Fish and Wildlife Conservation, Virginia Tech University, Blacksburg/Belize	Jaguars in Belize, population survey methods, global carnivore ecology, genetic capture-recapture
Sean Matthews	Conservation Scientist, Wildlife Conservation Society, Bozeman, Montana	Carnivore ecology, population estimation and spatial ecology, human-carnivore coexistence
Rodrigo Núñez	Projecto Jaguar, Puerto Vallarta, Mexico/Jalisco	Jaguars in Jalisco and Mexico
Tim O'Brien	Senior Conservation Scientist and Biostatistician, Wildlife Conservation Society, Bronx, New York	Quantitative wildlife population survey design and modeling
John Polisar	Jaguar Conservation Program Coordinator, Wildlife Conservation Society, Bronx, New York	Jaguars throughout their range, monitoring, human-jaguar coexistence, protected area management
Octavio Rosas-Rosas	Professor, Programa de Manejo y Conservacion de Fauna Silvestre, Colegio de Postgraduados, San Luis Potosi, Mexico	Jaguars in Sonora, , human-jaguar coexistence
Eric Sanderson	Senior Conservation Ecologist, Wildlife Conservation Society, Bronx, New York	Jaguar habitat modeling throughout the NRU, jaguar database construction
Rahel Sollmann	Post-doctoral Associate, North Carolina State University, Raleigh/Brazil	Jaguars in Brazil, quantitative wildlife population survey design and modeling

**APPENDIX 3:
SUMMARY OF THE APPLICATION OF TECHNIQUES**

How are jaguars distributed across a study area? What are the extremely coarse patterns of their abundance?

- *Use single-season occupancy models using program Presence (McKenzie et al. 2002, 2006; see [Presence-Absence and Occupancy](#))*

What proportion of an area is occupied by jaguars and their prey?

- *Use single-season occupancy models using program Presence (McKenzie et al. 2002, 2006; see [Presence-Absence and Occupancy](#))*

What are the environmental and management factors that influence jaguar distribution and abundance in an area?

- *This requires the inclusion of potential covariates in occupancy analyses.*
 - *Use survey sign frequency and recorded environmental and management parameters in transect segments when using foot-travelled and sign-based surveys – by transect within grid cell (using models developed in Hines et al. 2010, and deployed by Karanth et al. 2011a, Sunarto et al. 2012; see [Sign-based Occupancy Sampling for Jaguars](#))*
 - *Use remote-sensing-based parameters when using camera traps for occupancy (see [Covariates](#) subsection of [Presence-Absence and Occupancy](#))*
 - *The abundance-induced heterogeneity (Royle-Nichols) models can be used for crude estimates of jaguar abundance (see [Abundance-induced heterogeneity \(Royle-Nichols\) models](#) subsection of [Presence-Absence and Occupancy](#)), but can also be used for crude estimates of prey abundance (see [Occupancy Modeling for Prey Species](#)) – which also then serve as a template to understand jaguar distribution and abundance (see [Abundance and Density](#))*

What are the methods used to design and conduct adequate studies to measure trends in occupancy?

- *Use multi-season occupancy models using program Presence (McKenzie et al. 2003, 2006) to assess trends (see [Measuring Trends in Occupancy](#)), using single season pilot studies as input for power analyses, and conducting power analyses to evaluate effort needed to reach desired levels of confidence (see [Power Analysis](#))*

What are the methods used to measure numerical jaguar abundance and density with confidence?

- See [Abundance and Density](#)
- Use stationary camera-trap stations, following guidance in the text, and analyze using closed-population capture-recapture modeling: spatially explicit capture-recapture models (Gopalaswamy et al. 2012c, Royle et al. 2014)
- Use individually identified scats, following guidance in the text, then analyze using closed-population capture-recapture modeling via non-spatially explicit models, or spatially explicit capture-recapture models assigning scats located by search encounter into a grid system, thus transforming them into spatially stationary units, or via new models in development (Royle et al. 2011)
- Combine camera trap and genetic individual identifications (e.g, Gopalaswamy et al. 2012b)

What are the methods for measuring trends in abundance and density over time?

- See [Measuring Trends in Abundance/Density](#)
- Use non-spatially explicit robust-design open population capture-recapture modeling (Pollock 1982, Pollock et al. 1990, Kendall and Nichols 1995, Kendall et al. 1997) implemented in the program MARK (White and Burnham 1999)
- Use open SECR capture-recapture models formulated in the WINBUGS language (in development in 2014 – e.g. Gardner et al. 2010, Royle et al. 2014)

What are the methods for managing camera trap data?

- We provide guidance on the options for data recording for occupancy studies (see [Data Recording](#) subsection in *Presence-Absence and Occupancy*), and abundance and density studies (see [Data Recording](#) subsection in *Abundance and Density*), including recommendations on how to structure templates and design systems for efficient entry and retrieval/uptake for occupancy and density analyses

What are the methods for assessing jaguar demography, the patterns of survival and recruitment in my study area?

- See [Demographic Parameters and Spatial Ecology](#)
- Design and commit to long-term research sites
 - Use multi-year camera-trap data in conjunction with non-spatially explicit open population modeling repeated over years (Pollock 1982, Pollock et al. 1990, Karanth et al. 2006, 2011b, Pollock et al. 2012)

- *Analyze capture-recapture data using program MARK (White and Burnham 1999)*
- *Follow Karanth et al. (2011b) using the Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965) and Pollock's robust-design model (1982) to nest discrete closed population samples in an open long-term analysis to estimate survival and recruitment*
- *Use hierarchical spatial capture-recapture models using WINBUGS (Gardner et al. 2010)*
- *Use long-term known-fate collar data from at least 50-100 animals for survival analyses using the following models*
 - *Staggered entry Kaplan-Meier "known fates" option in MARK*
 - *Cox proportional hazard model (Cox 1972, Venables 1994, Riggs and Pollock 1992)*

What are the methods to use radio-telemetry to understand demographic parameters, dispersal, home range, and general spatial ecology of jaguars in a study area?

- *See [Home Range and Spatial Ecology](#)*
- *Frame research questions, study size and duration, and budget, then evaluate which vendors offer telemetry equipment adequate to address the questions. High initial investments lead to lower costs overall because failures are less frequent and study objectives are met. Demographic parameters will require large samples and multiple years to be meaningful, and any aspect of animal ecology requires time, so be prepared for years of research and plan accordingly*
- *Use home-range estimators that produce a utilization distribution describing the intensity of use of different areas*
- What are the methods used to obtain information about dispersal and long-distance movements?
 - *See [Dispersal and Long-Distance Movements](#)*
 - *This requires reliable telemetry equipment and a plan for a very large-scale study (Elbroch et al. 2009, Fattebert et al. 2013; see [Home Range](#))*
 - *Genetic tools can also be used to evaluate dispersal and long-distance movements (Gour et al. 2013, Forbes and Boyd 1996). See our section [Population Genetics](#) for technical advice and recommendations on collecting and processing samples*

- What are the methods used to evaluate patterns of habitat selection by jaguars in a study area?
 - See [Habitat Selection](#)
 - *In large-scale camera-trap-based occupancy sampling, remote sensing covariates provide abundant information about factors which may influence jaguar distribution (see [Covariates](#) subsection in Presence-Absence and Occupancy)*
 - *When environmental characteristics are recorded along segments of transects used for sign-based occupancy surveys for jaguars, the data can be used to model jaguar habitat selection (Sunarto et al. 2012; see [Sign-Based Occupancy Sampling for Jaguars](#))*
 - *When environmental parameters are recorded at each camera station in a capture-recapture study for jaguars, that data can be used for an analyses of habitat selection (Apps et al. 2006)*
 - *In large-scale telemetry studies, remote sensing can provide useful covariates to test as crude environmental characteristics influencing how jaguars use space (see [Covariates](#) subsection in Habitat Selection); however, there are ways to improve these analyses – the “habitat” data should be collected on the same time frame and on a similar level of resolution as the jaguar location data*
 - *Sign-based prey occupancy sampling described in Gopaldaswamy et al. (2012a) can be used to model the fine-grained patterns of prey distribution and abundance across the study area*
 - *Distance sampling (Buckland et al. 2008) can be conducted along linear foot transects distributed across vegetation types in the study area for a high-resolution assessment of total prey abundance and biomass, and also to provide a foundation for comparative value of habitats in terms of prey resources*
 - *We recommend that the fine grained real-time data obtained through telemetry be matched with vegetation and prey distribution data of similar resolution to maximize understanding of the habitats and resources selected by study animals (see [Conclusion](#) subsection in Habitat Selection)*
- What information is available in population genetics data and how are samples collected and processed?
 - *Population genetics reveals patterns of gene flow within and among landscapes that cannot be discerned by any other method (Andreasen et al. 2012). Beyond*

invisibly tracking relatedness inside individual jaguar conservation units, or across huge sections of jaguar range, population genetics analyses also provide estimates of heterozygosity, potential inbreeding, sub-division among populations, and increase our understanding of the evolution of the species on a range-wide scale (Eizirik et al. 2001, 2008, Ruiz-Garcia et al. 2009)

- *We provide technical advice on [Jaguar Scat Collection](#), [sampling using scat-detection dogs](#), [laboratory genetic methods](#), and [analysis of jaguar scat genetic data](#)*
- How are jaguar data recorded, stored, and processed on a large scale, e.g., the NRU, or range wide?
 - *Based on experience gained developing testing a platform for the entire NRU, we offer general and global recommendations on [data capture and curation](#), offering recommendations on data collection and export, standardization and aggregation, and editing and ingestion*
- How can we monitor the status of jaguars in the NRU and range wide?
 - *We summarize the recommendations generated by our team in the section [Recommendations and Guidelines for Northwestern Recovery Unit and Beyond](#)*

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**APPENDIX 4:
DIRECT JAGUAR AND PUMA OBSERVATIONS**

N°: _____		DIRECT JAGUAR AND PUMA OBSERVATIONS					
TO DESCRIBE THE ANIMAL/S	<i>Jaguar</i> <input type="checkbox"/>			<i>Puma</i> <input type="checkbox"/>	TO DESCRIBE DE PLACE		
	<i>Other:</i> _____				Location		
Color					GPS: _____ / _____		
Size							
Other characteristics					Place characteristics		
Number of	<i>Male</i>	<i>Female</i>	<i>Unknown</i>		Weather conditions		
<i>Adults</i>							
<i>Juvenile</i>							
<i>Cubs</i>							
TO DESCRIBE THE OBSERVATION	Date	Time	Term	Distance to the animal	Comments of the observer		
Other information collected	<i>Tracks</i>	<i>Feces</i>		<i>Other</i>			
Direct observer	Complete name		Post address / e-mail		Phone		
Person that complete the sheet	Complete name		Phone / e-mail		Comments of the colaborator		

Nº: _____

DIRECT JAGUAR AND PUMA OBSERVATIONS

TO DESCRIBE THE ANIMAL/S	Jaguar <input type="checkbox"/>	Puma <input type="checkbox"/>	TO DESCRIBE DE PLACE		
	<i>Other:</i> _____		Location		
Color			GPS: _____ / _____		
Size			Place characteristics		
Other characteristics					
Number of	<i>Male</i>	<i>Female</i>	<i>Unknown</i>		
<i>Adults</i>					
<i>Juvenile</i>					
<i>Cubs</i>					
TO DESCRIBE THE OBSERVATION	Date	Time	Term	Distance to the animal	Comments of the observer
Other information collected	<i>Tracks</i>	<i>Feces</i>	<i>Other</i>		
Direct observer	Complete name		Post address / e-mail		Phone
Person that complete the sheet	Complete name	Phone / e-mail		Comments of the colaborator	

Nº: _____

FICHA DE REGISTRO DE AVISTAJES

CARACTERÍSTICAS DEL ANIMAL	Yagareté <input type="checkbox"/>		Puma <input type="checkbox"/>		CARACTERÍSTICAS DEL LUGAR	
		Otro: _____				Ubicación
Color					Punto GPS: _____ / _____	
Tamaño					Características del lugar	
Señas particulares					Condiciones del tiempo	
Cantidades	Macho	Hembra	Desconocido			
Adulto						
Juvenil						
Cría						
DESCRIPCIÓN DEL AVISTAJE	Fecha	Hora	Duración	Distancia del observ.	Comentarios	
Anexos al registro	Huellas	Heces	Otros			
Datos del observador directo	Nombre completo		Dirección postal / e-mail		Teléfono	
Datos del tomador del registro	Nombre		Teléfono / e-mail		Comentarios del tomador del registro	

Nº: _____

FICHA DE REGISTRO DE AVISTAJES

CARACTERÍSTICAS DEL ANIMAL	Yagareté <input type="checkbox"/>	Puma <input type="checkbox"/>		CARACTERÍSTICAS DEL LUGAR	
	Otro: _____			Ubicación	
Color			Punto GPS: _____ / _____		
Tamaño			Características del lugar		
Señas particulares			Condiciones del tiempo		
Cantidades	<i>Macho</i>	<i>Hembra</i>			<i>Desconocido</i>
<i>Adulto</i>					
<i>Juvenil</i>					
<i>Cría</i>					
DESCRIPCIÓN DEL AVISTAJE	Fecha	Hora	Duración	Distancia del observ.	Comentarios
Anexos al registro	Huellas	Heces	Otros		
Datos del observador directo	Nombre completo		Dirección postal / e-mail		Teléfono
Datos del tomador del registro	Nombre	Teléfono / e-mail		Comentarios del tomador del registro	

**APPENDIX 5:
COLLECTING DATA ON TRACKS AND SCATS**

Sheet to photograph next to the footprints

JAGUAR AND PUMA TRACKS								
<i>Track Num.:</i> ___ <i>Date:</i> ____/____/____								
<i>Place:</i> _____								
<i>GPS:</i> _____/_____								
<i>Collector:</i> _____								
<i>Notes:</i> _____								
1	2	3	4	5	6	7	8	9

Label to stick on paper bags to collect feces

FECES OF JAGUARS AND PUMAS	
<i>Sample N°:</i> ___ <i>Date:</i> // .	
<i>Place:</i> ..	
<i>GPS:</i> ___ / ____.	
<i>Collector:</i> _____.	
<i>To describe the place:</i> river/stream – marsh near a house or building – forest – shrubs pastures – crops – road – trail	
<i>Notes:</i> ..	
_____.	
_____.	
_____.	
<i>Keep in a dry, ventilated place until process the sample</i>	

Ficha para fotografiar junto a las huellas

HUELLAS DE JAGUAR Y PUMA								
<u>Nro. Huella:</u> <u>Fecha:</u> ____/____/____								
<u>Lugar:</u> _____								
<u>Punto GPS:</u> _____/_____								
<u>Colector:</u> _____								
<u>Observaciones:</u> _____								
1	2	3	4	5	6	7	8	9

Etiqueta para pegar en las bolsas de papel para coleccionar heces

COLECTA DE HECES DE JAGUAR Y PUMA	
<u>Nro. Muestra:</u> _ . <u>Fecha:</u> // .	
<u>Lugar:</u> _ .	
<u>Punto GPS:</u> ____ / ____ .	
<u>Colector:</u> ____ .	
<u>Tipo de Ambiente:</u> río/arroyo – bañado	
cerca de vivienda – bosque/selva – arbustal	
potrero – cultivo – camino – sendero	
<u>Notas:</u> _ .	
_____ .	
_____ .	
_____ .	
<i>Mantener en un lugar seco y aireado hasta procesar la muestra</i>	

**APPENDIX 6:
EXAMPLE CAMERA SETUP DATA SHEET**

SITE: HILL BANK-Rio Bravo Conservation & Management Area
May-August 2012 - CODE 4RBHB2012 - Jaguar Survey

Station	Camera #s	Physical location	Date (m/d/y)	GPS location Easting (UTM X)	GPS location Northing (UTM Y)	Road (R), Trail (T), New Trail (NT), Game Trail (G), Skid Road	Width of road or trail (m)	Distance from Camera to middle of road or trail (m)	Canopy cover (%) at station **	Land use ***	Habitat type ****	Notes
4RBHB 01												
4RBHB 02												
4RBHB 03												
4RBHB 04												
4RBHB 05												
4RBHB 06												

* Human use: very high = >1 per day, high = 4-7/week, med= 1-3/week, low = < 1/week, zero = only camera work. ** Canopy cover: 0 = 0-10%, 10 = 10-20%, 20 = 20-30%, 30 = 30-40%, 40 = 40-50%, 50 = 50-60%, 60 = 60-70%, 70 = 70-80%, 80 = 80-90%, 90 = 90-100%. ***Land use: P pasture, C crops, PL plantation, PA protected area, PR Private Land, R roads, BA built up area. ****Habitat: FB broadleaf forest, FP palm forest, G grassland, B brushland, WG wooded grassland, M mangrove, FS Fresh water swamp, SS saline swamp, R riverine, P Playa (beach) (/transition between types)

**APPENDIX 7:
EXAMPLE CAMERA CHECKING DATA SHEET**

Site: Rio Bravo Conservation and Management Area - Hill Bank: 4RBHB - May 2012 - August 2012 - Jaguar survey

Survey Name: Check mark for things checked, Y or N for answers, dash for things not needing checking

Station Code RBHB = Hill Bank RBLM = La Milpa	Camera type & number BSS = BLK Moultrie MTD = Camo Moultrie RM = Reconyx RM45 HC = Reconyx HC500	Init camera checkers	Today's Date (m/d/y)	Trigger with station #, camera #, and date on display card	# Pics taken	Open camera, press off button, remove card	Battery level % for digital cameras	Change Batteries? Yes (Y) NO (N)	Which batteries changed? AAs, Cs, Ds	Card swapped out? Yes (Y) or No (N)	Digitals on still picture mode (S) or video mode (V)	Image Quality? High (H), Med (M), Low (L)	Event Delay in minutes	# pictures per event	Check date/time stamp on camera- is it correct?	Clean O-rings (camera seal) with cloth or alcohol prep pad	Clean lens cover, flash cover, and sensor cover	Set, lock, and reposition	Make sure camera is on (AUTO for MTs or switch for REs)	Trigger with station #, camera #, and date on display card	Notes - include anything out of the ordinary, damage to cameras by animals, suspected malfunctions, physical location if you change a camera location etc.
4RBHB																					
4RBHB																					
4RBHB																					

**APPENDIX 8:
EXAMPLE CAMERA TEST CARD**



Date: _____

Camera
Station: _____

Camera ID: _____



**APPENDIX 9:
EXAMPLE PHOTO-CAPTURED JAGUARS DATA SHEET**

Jaguars: Firbeburn Reserve, Belize

J90

Male

J91

male



date	time	x-location	y-location	place	date	time	x-location	y-location	place
08/07/07	14:56	0377210	2009269	C6	08/03/07	9:49	0375193	2007569	C10
08/09/07	21:03	0375193	2007569	C10	08/03/07	9:10	0375027	2005851	C16
07/31/07	22:35	0375193	2007569	C10	09/02/07	14:49	0374202	2004163	C22
08/04/07	6:59	0375193	2007569	C10	07/31/07	21:13	0374202	2004163	C22
08/28/07	7:29	0369451	2000916	C11					
08/01/07	9:05	0370319	2003233	C14					
08/04/07	7:41	0375027	2005851	C16					
08/09/08	20:23	0375027	2005851	C16					
08/15/07	14:31	0375027	2005851	C16					
08/31/07	21:56	0375027	2005851	C16					
08/04/07	8:26	0374202	2004163	C22					
08/08/07	15:12	0374202	2004163	C22					
08/09/08	19:42	0374202	2004163	C22					
09/13/07	14:36	0374202	2004163	C22					
08/28/07	14:39	0374202	2004163	C22					
06/30/07	8:13	0375043	2012516	N5					
05/22/07	22:54	0374354	2013205	N13					